THE EXTINCT CALIFORNIA TURKEY, *MELEAGRIS CALIFORNICA*, FROM RANCHO LA BREA: COMPARATIVE OSTEOLOGY AND SYSTEMATICS

ZBIGNIEW M. BOCHEŃSKI[1] AND
KENNETH E. CAMPBELL, JR.[2]

ABSTRACT. An extensive study of the comparative osteology of turkeys (Aves: Meleagrididae) confirms the validity of the extinct California Turkey, *Meleagris californica*. The study included all major and many minor skeletal elements of adult specimens of *M. californica*, best known from the asphalt deposits at Rancho La Brea, California, and both species of extant turkeys: *Meleagris gallopavo* and *Meleagris ocellata*. The study also confirmed that *M. californica* is more closely related to *M. gallopavo* than to *M. ocellata*. A review of turkey remains from localities other than Rancho La Brea confirmed the presence of *M. californica* in California within a relatively small geographic range extending from Orange County in the south, through Los Angeles County, to Santa Barbara County in the north. Other, unconfirmed records of fossil turkeys in the western United States suggest that the species might have been more widespread. Based on a unique combination of characters, we confirmed the presence of *Meleagris crassipes* in Howell's Ridge Cave, Grant County, New Mexico, which indicates that the geographic range of this extinct species extended from northeastern Mexico (San Josecito Cave) to at least New Mexico in the late Pleistocene. The close osteological similarity between *M. californica* and *M. gallopavo* suggests that the ancestors of *M. californica* became isolated in California only after nearing the *M. gallopavo* grade, but certain osteological features suggest different adaptations in the two species following divergence of their respective lineages. The high incidence of entrapment in the La Brea asphalt seeps is linked to the species' social behavior. The end Pleistocene extinction of *M. californica* might have resulted from the coincidental occurrence of two factors: a dramatic drop of precipitation to well below modern precipitation levels beginning about 11,500 BP, which would have concentrated local populations of turkeys around limited roost sites and water supplies, and the arrival of paleoindians in California, who might have hunted the concentrated birds to extinction.

INTRODUCTION

Of all the species of birds known from Rancho La Brea, the extinct California Turkey, *Meleagris californica* (L. Miller, 1909), is the second most common species, outnumbered only by the Golden Eagle, *Aquila chrysaetos* (Linnaeus, 1758). As many as 11,116 specimens attributable to *M. californica* and representing a minimum of 791 individuals have been identified in the Rancho La Brea fossil collections at the George C. Page Museum, a branch facility of the Natural History Museum of Los Angeles County. The specimens of the California Turkey, as with those of other animals from this site, are usually very well preserved, and all elements of the skeleton are represented, including such minor bones as wing and toe phalanges, vertebrae, and ribs. Another unusual feature characteristic of the Rancho La Brea turkey collection is the presence of a large number of immature specimens. Bones of young birds representing all stages of development from few-day-old chicks to nearly adult individuals are present. The material of juvenile turkeys has not yet been studied in great detail, but it has a great potential for research. For the most part, this study concerns only specimens from adult birds.

The description of *M. californica* and discussions about its possible relationship to modern turkeys have been the subject of several important studies over the past nearly 100 years. The difficulty and complexity of this task are reflected in the evolution of scientific names used to describe this species of bird. The species was first described as a peacock in the genus *Pavo* Linnaeus, 1758, by L. Miller (1909). A few years later, the same author created a separate genus, *Parapavo* L. Miller, 1916, for the species, arguing that it was intermediate between *Meleagris* [*Agriocharis*] *ocellata* Cuvier, 1820, of the Yuca-

---

[1] Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Slawkowska 17, 31-016 Cracow Poland; Post-doctoral Research Fellow, Vertebrate Zoology, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007 USA.
Email: bochenski@isez.pan.krakow.pl

[2] Vertebrate Zoology, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007, USA.
Email: kcampbell@nhm.org

Contributions in Science, Number 509, pp. 1–92
Natural History Museum of Los Angeles County, 2006

tan Peninsula of Central America and the genus *Pavo* of the Old World. Wetmore (1924), accepting the genus *Parapavo*, was the first person to recognize the extinct species as a turkey, intermediate between the modern *Meleagris* and *Agriocharis* Chapman, 1896. His conclusions were based on a study of the tarsometatarsus only. Howard (1927), in an analysis of all major skeletal elements, agreed with Wetmore (1924), but she considered *M.* [*Parapavo*] *californica* to be more similar to *M.* [*Agriocharis*] *ocellata* than to *Meleagris gallopavo*. In a later paper that concerned just the beak of the extinct species, Howard (1928) provided what she considered to be further evidence of the generic distinction of *M.* [*Parapavo*] *californica*. At the same time, Sushkin (1928), relying on his studies of the coracoid, carpometacarpus, and tarsometatarsus, argued that *M.* [*Parapavo*] *californica* was sufficiently similar to *M.* [*Agriocharis*] *ocellata* that it could be congeneric. Nevertheless, the genus *Parapavo* was widely accepted for more than 50 years (e.g., Wetmore, 1931; Brodkorb, 1964a, 1964b). Meanwhile, A. Miller and Bowman (1956) found no basis in the tarsometatarsus for a generic separation of *Parapavo* and *Meleagris*. In the last major review of the California Turkey, Steadman (1980) restudied all major skeletal elements, synonymized the genus *Parapavo* with *Meleagris*, and concluded that *M. californica* was more similar to *M. gallopavo* than to *M. ocellata*.

The two main studies that analyzed in detail all the major osteological elements of turkeys (i.e., Howard, 1927; Steadman, 1980) were focused on somewhat different problems. Howard (1927) compared four species, which, as it was thought at the time, represented four different genera (*Parapavo*, *Pavo*, *Meleagris*, and *Agriocharis*), whereas Steadman (1980) contrasted the two extant species of turkey with a number of fossil species, with *M. californica* being just one of them. All the other, less "in depth" papers on the California Turkey were based on comparisons with relatively few modern specimens. This is probably one of the reasons why the systematic status of *M. californica* underwent so many changes. At the beginning of this study it became obvious that individual variation within each of the three species (i.e., two extant and one extinct) is very large, and, therefore, any reliable research on this particular group of birds should be based on a large series of specimens.

Although historically less complicated than *Meleagris californica*, the systematic position of the Ocellated Turkey, *Meleagris* [*Agriocharis*] *ocellata*, also has been changed several times during its long history. Early in the nineteenth century it was described as *M. ocellata* Cuvier, 1820. It was then placed in the monotypic genus *Agriocharis* Chapman, 1896, which was widely accepted until late in the twentieth century, when it was moved back to *Meleagris* by Steadman (1980). Since that time, major reference works have listed it as *M. ocellata* (e.g., del Hoyo et al., 1994). Relatively little is known of this species, and our present knowledge of it is based on a few, often old publications. Many of the comparative osteological specimens available for research are birds derived from zoos, with all their unpredictable abnormalities relative to wild birds.

The goal of this research was to restudy the osteology of *M. californica* and compare and contrast it to that of the two living turkeys, *M. gallopavo* and *M.* [*A.*] *ocellata*, in order to clarify the systematic position of the fossil species and its relationship to the modern taxa. A second objective was to try to resolve problems connected with the origin and extinction of *M. californica*. We took this opportunity to address as well the question of the appropriate systematic position of *M.* [*A.*] *ocellata*, although we recognize that we did not have a sufficiently large sample of wild *M.* [*A.*] *ocellata* to measure adequately natural variation in this species.

MATERIALS AND METHODS

Before this study was undertaken, there were approximately 9,000 catalogued specimens of *M. californica* from the Rancho La Brea sites stored at the Page Museum. The study began with the curation of the fossil material, which revealed approximately 2,000 more specimens of turkeys among unidentified materials from both older collections and those of more recent periods of excavation, increasing the total number of known remains to 11,116, representing a minimum of 791 individuals. The specimens include all elements of the skeleton, including vertebrae and wing and toe phalanges. They came from 28 different excavation pits, but they are not distributed evenly among them. Over 51 percent of the 11,116 specimens came from Pit 16 and nearly 14 percent from Pit 4. Nine other excavation pits each contained 1–7 percent of the specimens, and the remaining 17 excavation pits each yielded well below 1 percent of the specimens. All the fossil turkey bones were included in the study, with the exception of some minor elements (e.g., most phalanges, vertebrae, and ribs), heavily damaged bones, and young, clearly incompletely ossified specimens.

Modern comparative osteological specimens of the Wild Turkey, *M. gallopavo*, used in this study represented both sexes of all five living subspecies. Most of the modern comparative specimens were supplied by the National Wild Turkey Federation, and all were obtained from the wild by fish and game offices and hunters from across the country. These specimens were prepared by bacterial maceration, catalogued into the Ornithology Collections of the Natural History Museum of Los Angeles County, and had all bones numbered prior to the initiation of the study. These specimens comprise the largest and most geographically comprehensive collection of the extant Wild Turkey in the world. In all, the following 51 specimens were examined: *M. gallopavo intermedia* (9 specimens: 4♀, 5♂), *M. gallopavo merriami* (11 specimens: 7♀, 4♂), *M. gallopavo mexicana* (10 specimens: 4♀, 6♂), *M. gallopavo osceola* (9 specimens: 4♀, 5♂), *M. gallopavo silvestris* (11 specimens: 4♀, 7♂), and one specimen of an unknown subspecies and sex.

Most specimens were complete skeletons. Except for differences in size, no consistent morphological differences between subspecies were observed. Therefore, in the descriptions of the osteological characters, we made no distinction among subspecies.

Most of the 20 modern skeletons of the Ocellated Turkey, *M. ocellata* (5 ♀, 10 ♂, 5 sex?), available for the study were from zoo birds rather than wild birds, and their osteological features might well have been affected by a "zoo lifestyle." Unfortunately, many of the specimens were also partial skeletons. They came from the following five collections: Natural History Museum of Los Angeles County (LACM); Dickey Collection at the University of California, Los Angeles (UCLA); Museum of Vertebrate Zoology, University of California, Berkeley (UC MVZ); San Diego Natural History Museum (SD NHM); and Museum of Zoology, University of Michigan (UMMZ).

All skeletal elements included in the study were carefully examined for unique morphological characters that would distinguish the three species involved. The characters studied included size, shape, position of bone structures, and the attachment scars of muscles and tendons. The term "state" used in the description of characters refers to the two (sometimes three) possible options within each described character (e.g., presence or absence of a structure, various shapes of a particular part of a bone, and so on). States of each character are designated by capital letters (i.e., State A, State B, and so on).

Early on in the study it became apparent that finding good osteological characters differentiating each of the species would be extremely difficult because of the very large degree of individual variation and an overall similarity between the species. For that reason, only the characters that occurred in at least 66 percent, or two-thirds, of all the specimens of one species were taken into consideration in the present study. This was a useful compromise that allowed us to describe more than just a few nearly perfect osteological characters that always differed among the species. When applied cautiously, preferably in combination with other characters, less-than-perfect characters are sufficiently reliable to be useful in identification of bones to species. This "66 percent rule" was also used in two other osteological monographs (Bocheński, 1994; Tomek and Bocheński, 2000). It seems to be more fair to address clearly the problem of variation in this way rather than working around it in the text by using such vague terms as "most specimens," "usually," or something similar. Of the nearly 100 working characters initially identified as potentially useful for separating the various bones of the three species, only about half fulfilled the "66 percent rule" and were considered valid at the end of the study.

In the "Comparative Osteology" section, where the osteological characters are described, the data following the name of each species include the percentages of specimens that show the particular state and the total number of specimens examined (e.g., "A = 75%, N = 40" means that 75 percent of the 40 specimens examined showed the "A" state; the remaining specimens of the species were of the opposite or an intermediate state).

All characters are illustrated in digital photographs taken by Kenneth E. Campbell, Jr. Prior to being photographed, all fossil and many modern specimens were lightly coated with ammonium chloride (NH_4Cl) to facilitate character illustration. The photographs were then edited and assembled into plates using Adobe Photoshop and Corel Photo-Paint.

For the most part, anatomical terminology follows Baumel et al. (1993), but sometimes terminology from Baumel et al. (1979) and the works of Howard (1980) and Gheţie et al. (1976) were adopted. All scientific terms used in this paper are labeled in the photographs illustrating the characters described.

Up to ten measurements were defined on each bone. The measurements taken, which are illustrated in black-and-white drawings, depended partly on the preservation of the fossils and partly on their possible usefulness in distinguishing the three species of turkey. All the fossil specimens of less numerous elements (e.g., parts of the axial skeleton, some long bones) were measured. However, in the case of particularly numerous fossil elements (e.g., tarsometatarsi, tibiotarsi, and carpometacarpi), only a large sample of bones was measured. This sample usually included all bones of the right side (complete and fragmentary), plus, in some instances, all complete bones of the left side. All measurements were made using digital calipers accurate to 0.01 mm, and all data were captured directly to computer. The measurements were stored, and the basic statistics, including minimum, maximum, arithmetic mean, and standard deviation, were computed in Microsoft Excel. In the case of *M. gallopavo*, the mensural data are presented in multiple ways: for each subspecies separately (sexes pooled), for each sex separately (subspecies pooled), and for all specimens of the species (with all subspecies and sexes pooled). Illustrations of the measurements taken appear in the Appendix, Figures A1–A7. Mensural data appear in the Appendix, Tables A1–A15. A database that includes a list of all fossil and modern specimens measured and their raw measurements is stored at the George C. Page Museum.

All bones were checked for ratios that could be used to differentiate the three species. Useful ratios of two measurements were found on several elements, and the scatter diagrams of the measurements were prepared using Microsoft Excel and Corel Photo-Paint.

Turkey remains from all other localities of the Irvingtonian, Blancan, and Rancholabrean North American Land Mammal Ages stored in the Vertebrate Paleontology Section of the Natural History Museum of Los Angeles County were checked for the characters found on the three main species investigated. Of the materials studied, those of *Meleagris crassipes* L. Miller, 1940, from San Josecito Cave, Mexico, seem to be of special importance for the understanding of the possible origin of *M. californica*. Unfortunately, time constraints did not permit an in-depth study of this material; our brief examination of the remains allows us to merely recognize the problem.

COMPARATIVE OSTEOLOGY

PREMAXILLA

The characters of the beak (Fig. 1) distinguish *M. californica* from the modern turkeys, with *M. gallopavo* and *M. ocellata* being indistinguishable from each other. The premaxillae of *M. californica* are shorter, wider, and flatter than those of the two modern species (characters 1 and 2). Moreover, in *M. californica* the Processus maxillaris is relatively wider (character 3), and the internal, posterior openings in the premaxillae are

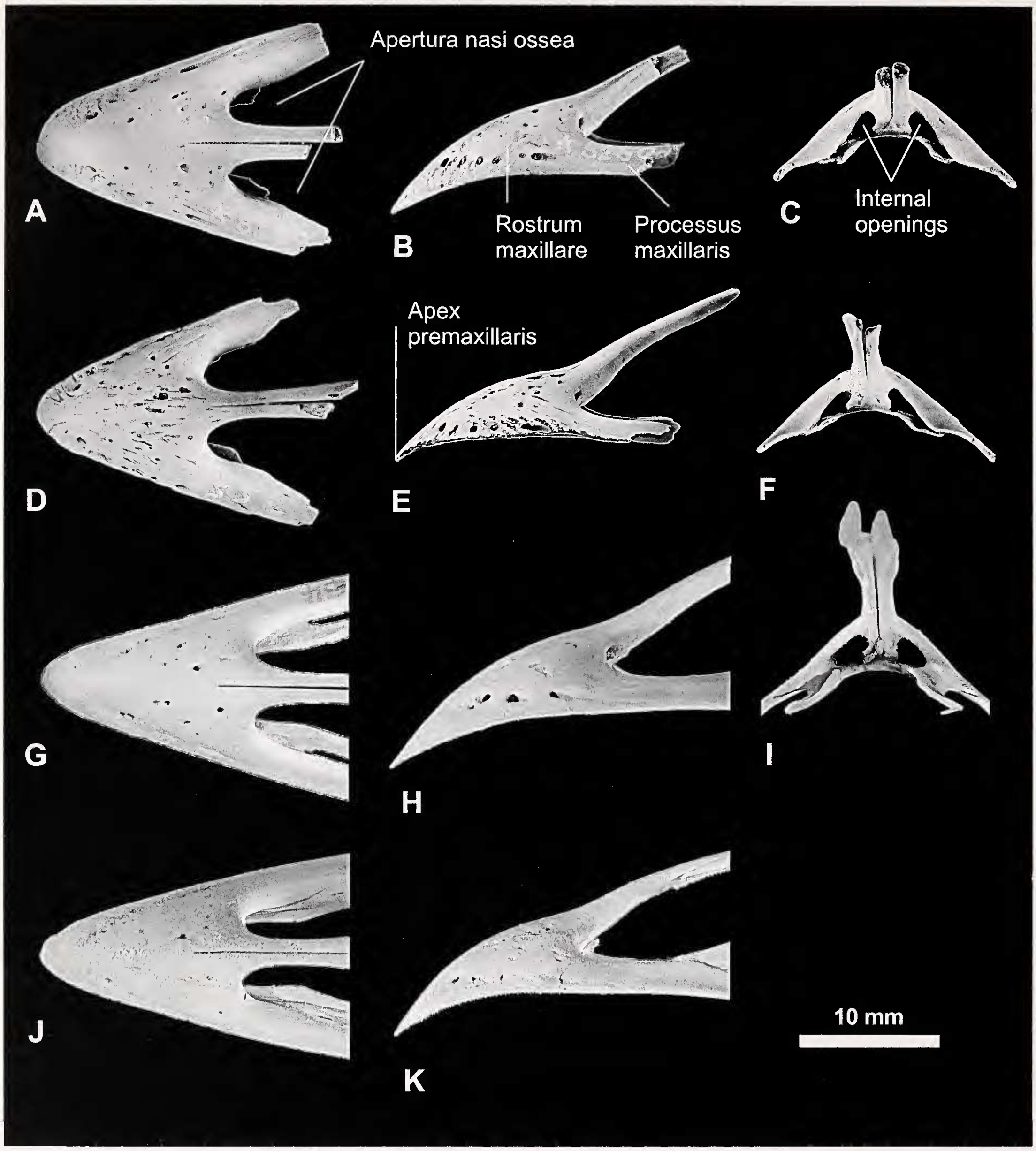


Figure 1 Premaxilla in dorsal, lateral, and posterior views. *Meleagris californica* (two specimens: A–C, LACMHC K8260; D–F, LACMHC F3225); *M. gallopavo* (G–I, LACM 112164); *M. ocellata* (J–K, UMMZ 151343; posterior view could not be illustrated without damaging the bones because in all available specimens of *M. ocellata* beaks were attached to the braincase). The beak of *M. californica* is shorter, wider and flatter than that of the two modern species. Also, in *M. californica* the two internal openings (views C and F *vs.* I) are narrower, and the Processus maxillaris is wider relative to length of Rostrum maxillare.

narrower (character 4) than the corresponding openings in the extant species.

CHARACTER 1. Dorsal view [redefined from Howard (1928) and Steadman (1980)].

State A (*M. ocellata*: 81%, N = 16; and *M. gallopavo*: 97%, N = 39): Premaxilla at the anterior tip of external nares (Apertura nasi ossea) is narrow relative to its length; its width at anterior tip of external nares is clearly less than its length from external nares to tip (Apex premaxillaris). The ratio of measurements B:A (Fig. A1) is ≤ 0.8.

State B (*M. californica*: 100%, N = 23): Premaxilla is wide relative to its length (the width is nearly equal to the length); the ratio of measurements B:A is ≥ 0.9.

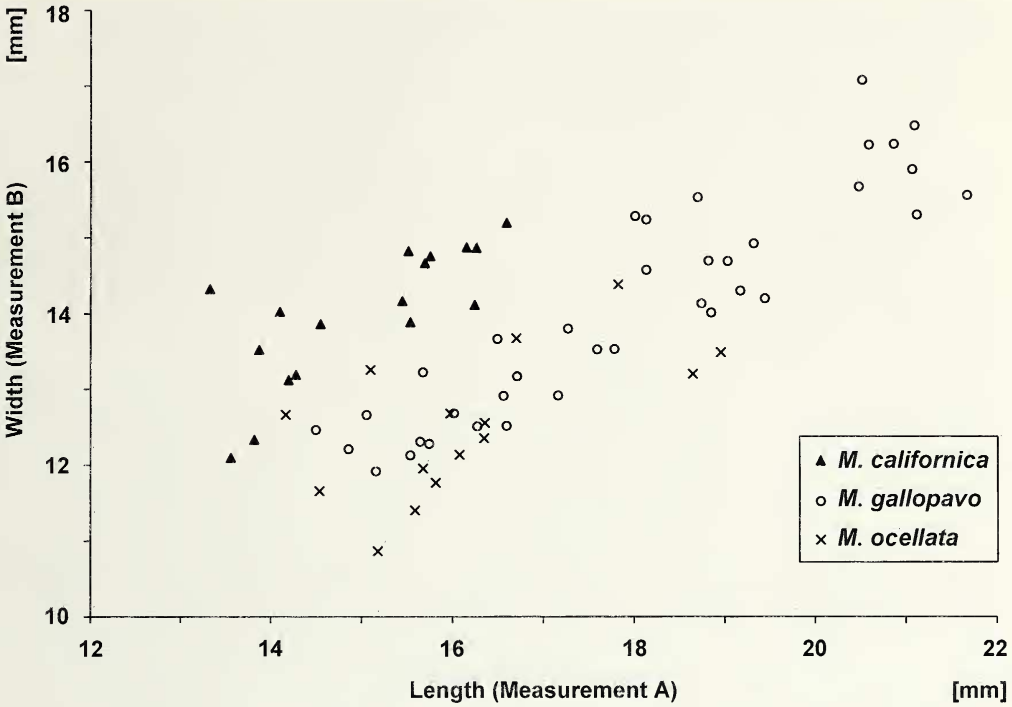


Figure 2 Premaxilla: Scatter diagram of measurements A and B (refers to premaxilla character 1, Table A1, and Fig. A1). *Meleagris californica* has a relatively wide beak compared to that of the other two species, whereas the larger specimens of *M. gallopavo* are distinguishable from the other two species by their absolute size.

NB: See Table A1 for measurements and Figure 2 for scatter diagram of measurements A and B.

CHARACTER 2. Dorsal and lateral views [redefined from Howard (1928) and Steadman (1980)].

State A (*M. ocellata*: 94%, N = 17; and *M. gallopavo*: 95%, N = 40): The portion of the premaxilla (Rostrum maxillare) between the tip of the beak (Apex premaxillaris) and the external nares rises higher and slopes more steeply dorsally (relative to its width at the end of external nares) than in state B; the ratio of measurements C:B (Fig. A1) is ≥ 0.5. A central ridge extending from the tip of the beak to the external nares often can be discerned.

State B (*M. californica*: 88%, N = 24): Premaxilla is relatively lower and slopes less steeply dorsally; the ratio of measurements C:B is ≤ 0.4. No central ridge can be discerned as the bone rises smoothly and gradually.

NB: See Table A1 for measurements and Figure 3 for scatter diagram of measurements B and C.

CHARACTER 3. Lateral view.

State A (*M. ocellata*: 94%, N = 16; and *M. gallopavo*: 98%, N = 40): Processus maxillaris near the anterior tip of external nares is narrow relative to length of Rostrum maxillare; the ratio of measurements A:D (Fig. A1) is ≥ 4.6.

State B (*M. californica*: 90%, N = 21): Processus maxillaris near the anterior tip of external nares is wide relative to length of Rostrum maxillare; the ratio of measurements A:D is ≤ 4.5.

NB: See Table A1 for measurements and Figure 4 for scatter diagram of measurements A and D.

CHARACTER 4. Posterior view.

State A (*M. ocellata*: 76%, N = 17; and *M. gallopavo*: 82%, N = 40): The two internal openings leading into the premaxilla are broad.

State B (*M. californica*: 96%, N = 23): The dorsolateral edges of the two internal openings are occupied by narrow ridges that extend as flaps ventromediad, partially screening the openings.

MANDIBLE

The characters of the articular region of the mandibulae (Fig. 5) serve to distinguish those of *M. gallopavo* from those of the other two species of turkeys. In *M. gallopavo*, the Processus caudalis (caudal process) is relatively shallow compared to the Ramus mandibulae (mandibular ramus) (character 1), and the Processus mandibulae medialis (medial mandibular process) extends posteromediad at a greater angle to the mandibular ramus (character 2).

CHARACTER 1. Lateral view.

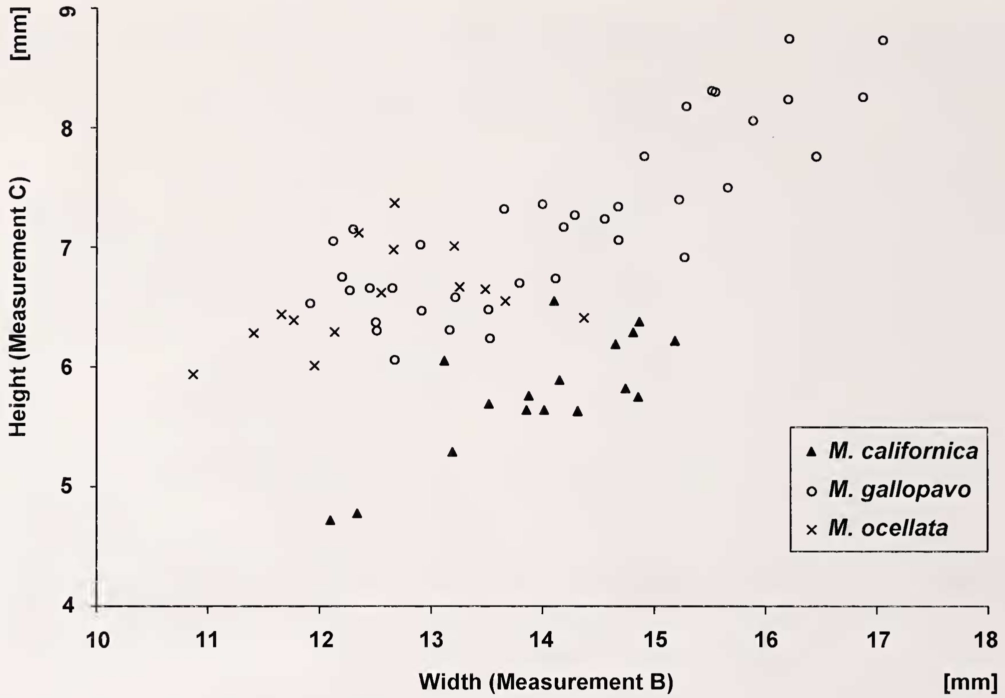


Figure 3 Premaxilla: Scatter diagram of measurements B and C (refers to premaxilla character 2, Table A1, and Fig. A1). In *M. californica*, the premaxilla is flatter than that in the two modern species.

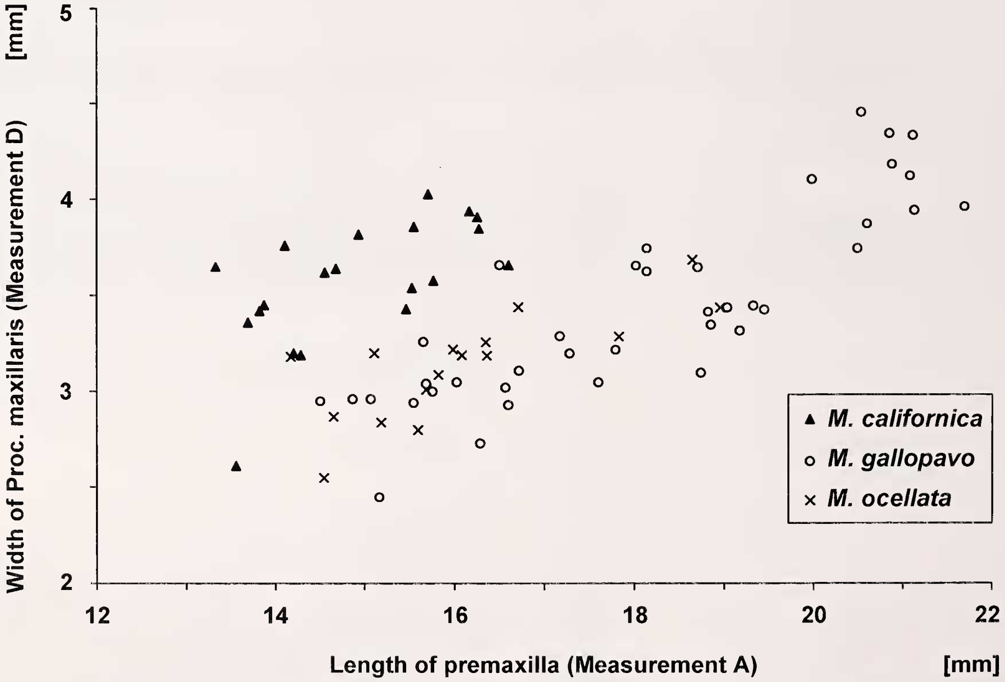


Figure 4 Premaxilla: Scatter diagram of measurements A and D (refers to premaxilla character 3, Table A1, and Fig. A1). The Processus maxillaris is relatively wider in *M. californica* than in the two modern species.

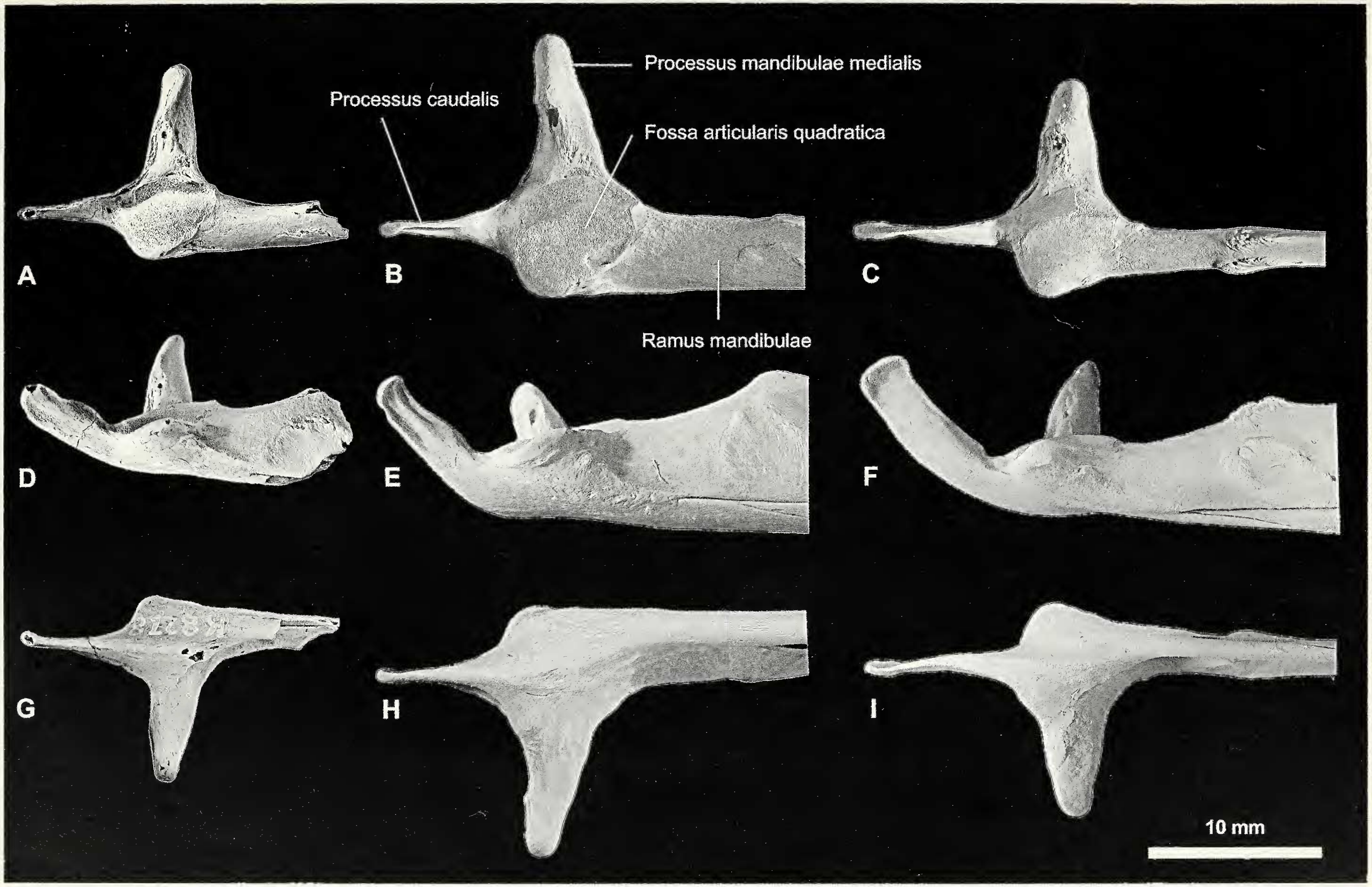


Figure 5 Mandible (articular portion, right side) in dorsal, lateral, and ventral views. *Meleagris californica* (A, D, and G, LACMHC K8278); *M. gallopavo* (B, E, and H, LACM 112165); *M. ocellata* (C, F, and I, UMMZ 151342). In *M. gallopavo*, the Processus caudalis is dorsoventrally narrow compared to the dorsoventral width of Ramus mandibulae (E *vs.* D and F), and Processus mandibulae medialis is at a wider angle to the Ramus mandibulae (B *vs.* A and C).

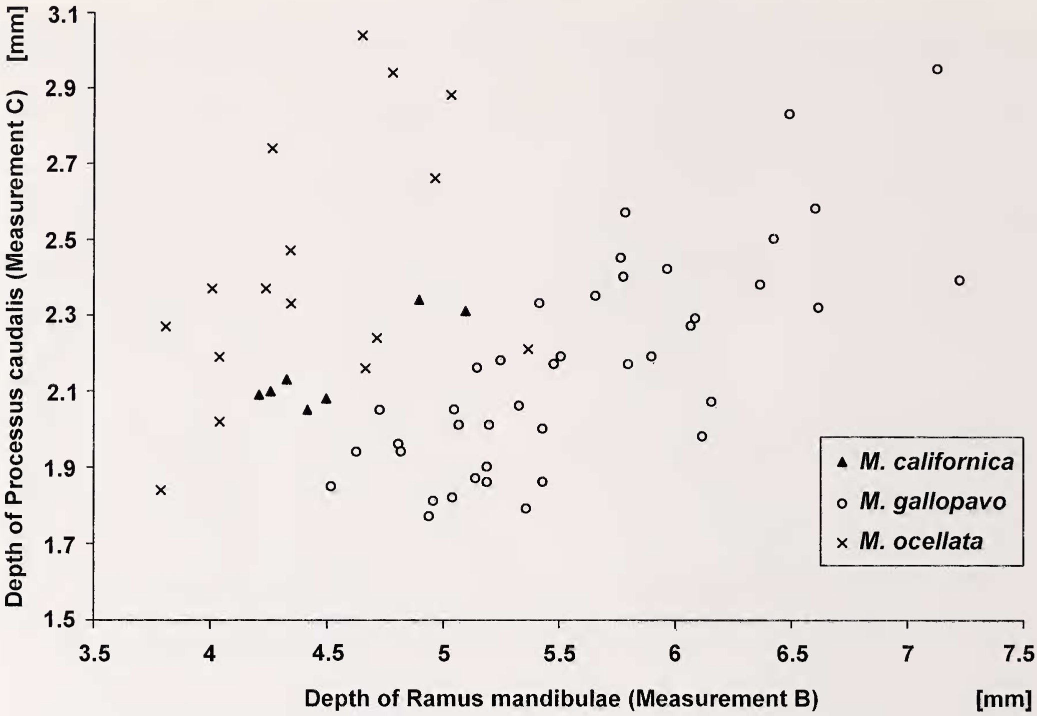


Figure 6 Mandible: Scatter diagram of measurements B and C (refers to mandible character 1, Table A2, and Fig. A1). In *M. gallopavo*, the Processus caudalis is relatively narrow compared to the width of the Ramus mandibulae. Although *M. californica* falls within the range of *M. ocellata*, many specimens of the latter species can be distinguished also.

State A (*M. gallopavo*: 98%, N = 41): Processus caudalis, measured at its narrowest dorsoventral point adjacent to the Fossa articularis quadratica, is relatively shallow [compared to the depth of the Ramus mandibulae distal to the Fossa articularis quadratica (Cotylae lateralis and medialis)]. The ratio of measurements B:C (Fig. A1) is ≥ 2.3.

State B (*M. ocellata*: 94%, N = 16; and *M. californica*: 100%, N = 7): Processus caudalis, measured at its narrowest dorsoventral point adjacent to the Fossa articularis quadratica (Cotylae lateralis and medialis), is relatively deep (compared to the depth of the mandibular ramus). The ratio of measurements B:C is ≤ 2.2.

NB: See Table A2 for measurements and Figure 6 for scatter diagram of measurements B and C. It is highly recommended that one rely on the ratio of measurements for this character rather than on a visual impression because of the large differences in size among specimens. Although only a few specimens of *M. californica* were available, it seems that their values of the B:C ratio are in the upper limit of those for *M. ocellata* (2.0–2.2 *vs.* 1.5–2.1, respectively), thus many specimens of *M. ocellata* can be distinguished from those of *M. californica* (Fig. 6).

CHARACTER 2. Dorsal view.

State A (*M. gallopavo*: 81%, N = 42): The angle between the Processus mandibulae medialis and the most posterior part of the Ramus mandibulae is significantly greater than 90 degrees.

State B (*M. ocellata*: 94%, N = 17; and *M. californica*: 78%, N = 9): The angle between the Processus mandibulae medialis and the most posterior part of the Ramus mandibulae is close to 90 degrees.

QUADRATUM

Two characters of the quadratum (Fig. 7), which are a relatively short Processus oticus (character 1) with a relatively small bulge (character 2), distinguish *M. ocellata* from the other two species.

CHARACTER 1. Lateral view.

State A (*M. ocellata*: 88%, N = 17): The length of Processus oticus is equal to or only slightly longer than the length of Processus mandibularis.

State B (*M. gallopavo*: 100%, N = 38; and *M. californica*: 71%, N = 14): The length of Processus oticus is clearly greater than the length of Processus mandibularis.

NB: This character relies on visual impression because it is not possible to determine one point

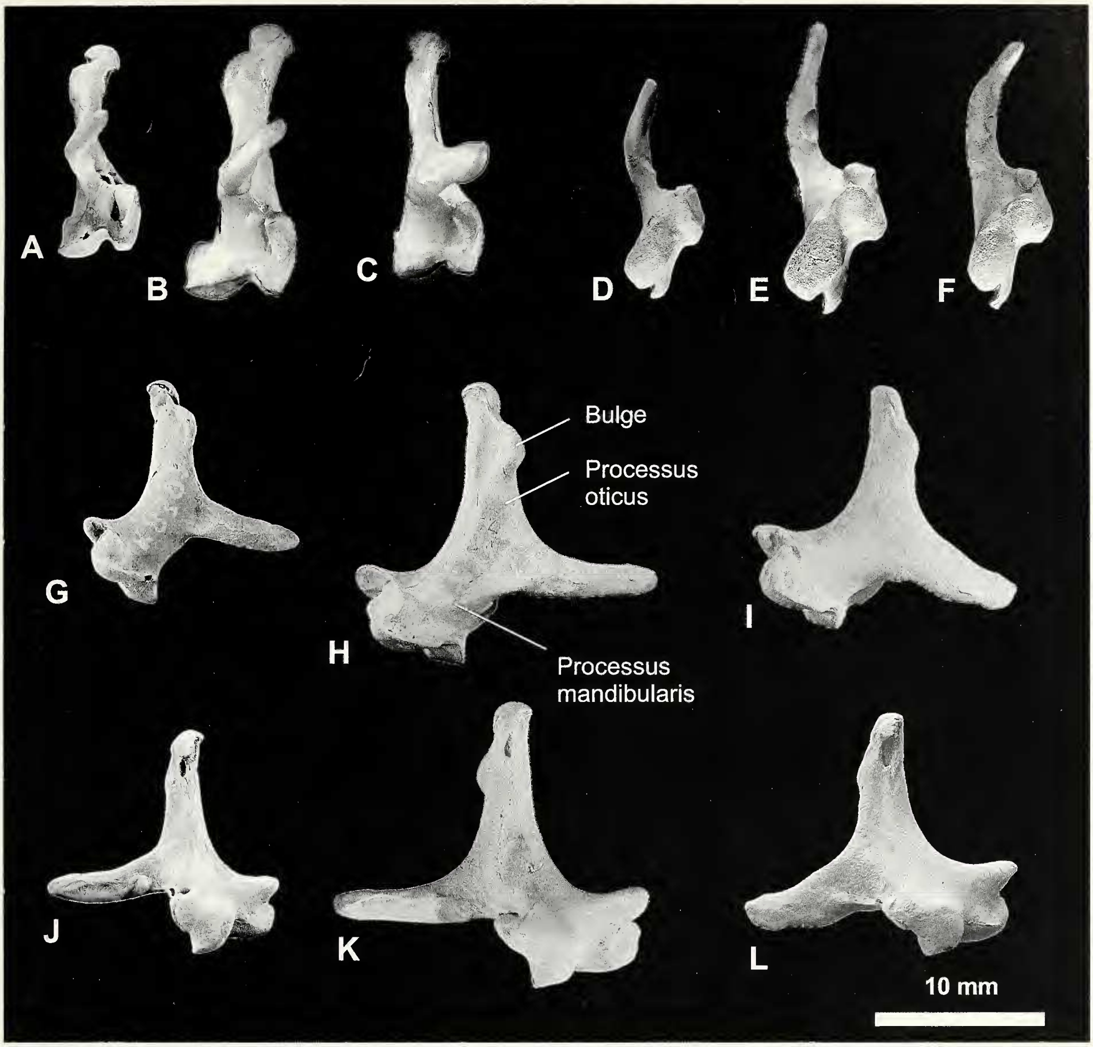


Figure 7 Right quadratum in various views. *Meleagris californica* (A, D, G, and J; LACMHC K8302); *M. gallopavo* (B, E, H, and K; LACM 112167); *M. ocellata* (C, F, I, and L; LACM 88937). In *M. ocellata*, the Processus oticus is almost as long as the Processus mandibularis, and the bulge on Processus oticus is relatively small (both characters: I *vs.* G and H).

from which the lengths can be measured. The four specimens of *M. californica* that differ from the others belong to young individuals.

CHARACTER 2. Lateral view.

State A (*M. ocellata*: 88%, N = 17): The bulge on the medial surface of Processus oticus near its end is small.

State B (*M. gallopavo*: 95%, N = 38; and *M. californica*: 100%, N = 7): The bulge on the medial surface of Processus oticus near its end is large; it clearly projects beyond the orbital edge of the otic process.

NB: All six immature specimens of *M. californica* show State A, which suggests that the bulge develops with maturation. These specimens were not included as representatives of this character.

SKULL

Only two characters of the skull (Fig. 8) distinguish *M. ocellata* from the other two species. In *M. ocellata*, the Processus postorbitalis projects less laterad (character 1), and the anteromedial process of the Lamina parasphenoidalis (basitemporal plate) points dorsad (character 2).

CHARACTER 1. Posterior view [redefined from Howard (1927) and Steadman (1980)].

State A (*M. ocellata*: 85%, N = 13): The Processus postorbitalis projects less laterad than the most lateral part of the Margo supraorbitalis, although sometimes it approximates the extent of the latter.

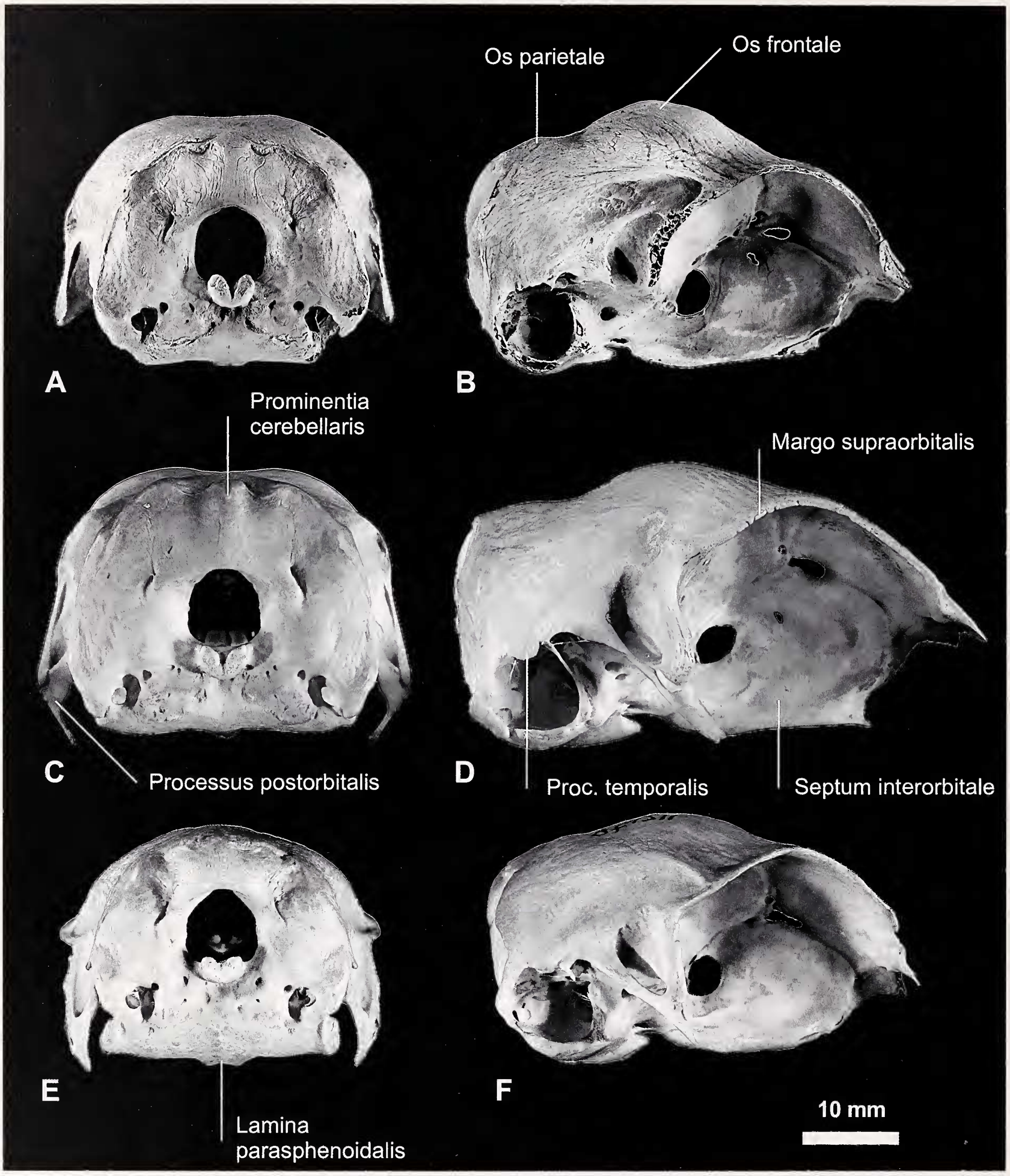


Figure 8 Skull in posterior and lateral views. *Meleagris californica* (**A**, **B**; LACMHC E7750; *M. gallopavo* (**C**, **D**; LACM 112165); *M. ocellata* (**E**, **F**; LACM 112170; (**F** is flipped to show left side because right orbit is damaged). In *M. ocellata*, the Processus postorbitalis projects less, or only as much, laterad than the most lateral part of the Margo supraorbitalis (E *vs*. A and C), and the anterior process of the basitemporal plate (Lamina parasphenoidalis) points dorsad rather than toward the beak (F *vs*. B and D). The eye-catching differences in the shape of the transition between Os frontale and Os parietale (B, D, F) have proved not to be species specific and are considered to be an expression of individual variation.

State B (*M. gallopavo*: 85%, N = 39; and *M. californica*: 88%, N = 16): The Processus postorbitalis projects farther laterad than the most lateral part of the Margo supraorbitalis.

CHARACTER 2. Lateral view.

State A (*M. ocellata*: 81%, N = 16): The anteromedial process of the basitemporal plate (Lamina parasphenoidalis) points, or curves, dorsad. This character state is probably connected with the fact that the Septum interorbitale does not extend as far ventrad as in State B.

State B (*M. gallopavo*: 98%, N = 40; and *M. californica*: 100%, N = 13): The anteromedial process on the basitemporal plate points toward the beak, which probably reflects the fact that the Septum interorbitale extends farther ventrad than in State A.

FURCULA

The furcula is one of the most diagnostic elements in terms of the number of characters described (Fig. 9). Although most of the characters are very good and easy to identify, in two (i.e., characters 3 and 5) the percentage of typical specimens is at the lower acceptable limit (i.e., around 66 percent) for some species, and therefore special caution in using them is advisable. All characters described are located in the region of the Apophysis furculae (hypocleideum) because only this portion is preserved in the fossil specimens; the possible differences between extant taxa on the scapular portion could not be compared with *M. californica*. Character 3 (crest on the hypocleideum) is species specific; the other characters divide the three species into two groups; that is, they distinguish one species from the other two. Typical of *M. californica* are intermuscular lines on the anterior side of the hypocleideum (character 5) and its bulging surface (character 6). Structures typical of *M. ocellata* include robust Corpus claviculae (rami) (character 1) and their outward curvature (characters 2 and 4).

CHARACTER 1. Sternal part, posterior view.

State A (*M. ocellata*: 87%, N = 15): Rami are massive and robust.

State B (*M. gallopavo*: 98%, N = 47; and *M. californica*: 92%, N = 12): Rami are relatively thin and lightly built.

CHARACTER 2. Sternal part, posterior view [redefined from Howard (1927) and Steadman (1980)].

State A (*M. ocellata*: 88%, N = 17): Rami near hypocleideum curve outward. The curvature is not great, but it is clear when compared with specimens of State B.

State B (*M. gallopavo*: 96%, N = 47; and *M. californica*: 100%, N = 12): Rami are straight.

CHARACTER 3. Sternal part, posterior view.

State A (*M. gallopavo*: 67%, N = 46): Crest on hypocleideum is elevated and broad throughout its length. It forks into two muscle lines, one going toward each of the rami. There is a bony "pocket" of variable size and shape at the dorsal end of the crest.

State B (*M. ocellata*: 87%, N = 15): Crest on hypocleideum is elevated and broad throughout its length. It forks into two muscle lines, one going toward each of the rami. A "pocket" is absent.

State C (*M. californica*: 100%, N = 14): Crest on hypocleideum slopes gradually toward the rami (i.e., it is not elevated at the dorsal end). It continues as a single muscle line going toward the juncture of the rami (i.e., it does not fork). A "pocket" is absent.

NB: Although there is some overlap between *M. gallopavo* and *M. ocellata*, with some specimens of *M. gallopavo* being of the *M. ocellata* type and vice versa, these two taxa are clearly separable from *M. californica* using this character.

CHARACTER 4. Sternal part, lateral view [redefined from Howard (1927) and Steadman (1980)].

State A (*M. ocellata*: 100%, N = 16): Rami near hypocleideum are straight or curve slightly anteriad (i.e., are concave).

State B (*M. gallopavo*: 78%, N = 46; and *M. californica*: 100%, N = 9): Rami near hypocleideum curve posteriad (i.e., are convex).

CHARACTER 5. Sternal part, anterior view [see Howard (1927) and Steadman (1980)].

State A (*M. ocellata*: 65%, N = 17; and *M. gallopavo*: 72%, N = 47): The hypocleideum and both rami near it are smooth (intermuscular lines are absent).

State B (*M. californica*: 64%, N = 11): Intermuscular lines extend from the hypocleideum to the beginnings of the rami.

CHARACTER 6. Sternal part, anterior view.

State A (*M. ocellata*: 100%, N = 15; and *M. gallopavo*: 70%, N = 47): The triangular surface of the hypocleideum, in anterior view, is flat or depressed.

State B (*M. californica*: 92%, N = 13): The triangular surface of hypocleideum bulges anteriad.

STERNUM

The sternum is one of the best elements in terms of the number of characters that distinguishes each species and their quality (Figs. 10a–c), and a well-preserved bone can be identified to the species level relatively easily. Most of the characters described are located in the rostral region because this part preserves best in fossils and can be compared across the three taxa studied. There might be more differences in the posterior part of the sternum between *M. ocellata* and *M. gallopavo*, but because of the scarcity of fossil specimens with the posterior part preserved, it was not possible to include *M. californica* in such comparisons. Character 5, shape of the Spina dorsale rostri, is species specific, and character 8, relative width of the sternum, distinguishes *M. ocellata* and *M. gallopavo*, with *M. californica* being intermediate. Each of the remaining characters divides the three species into two groups; that is, they distinguish one species from the other two. Typical of *M. californica* is a small Spina ventrale rostri on the Rostrum sterni (character 1). Structures typical of *M. gallopavo* include the

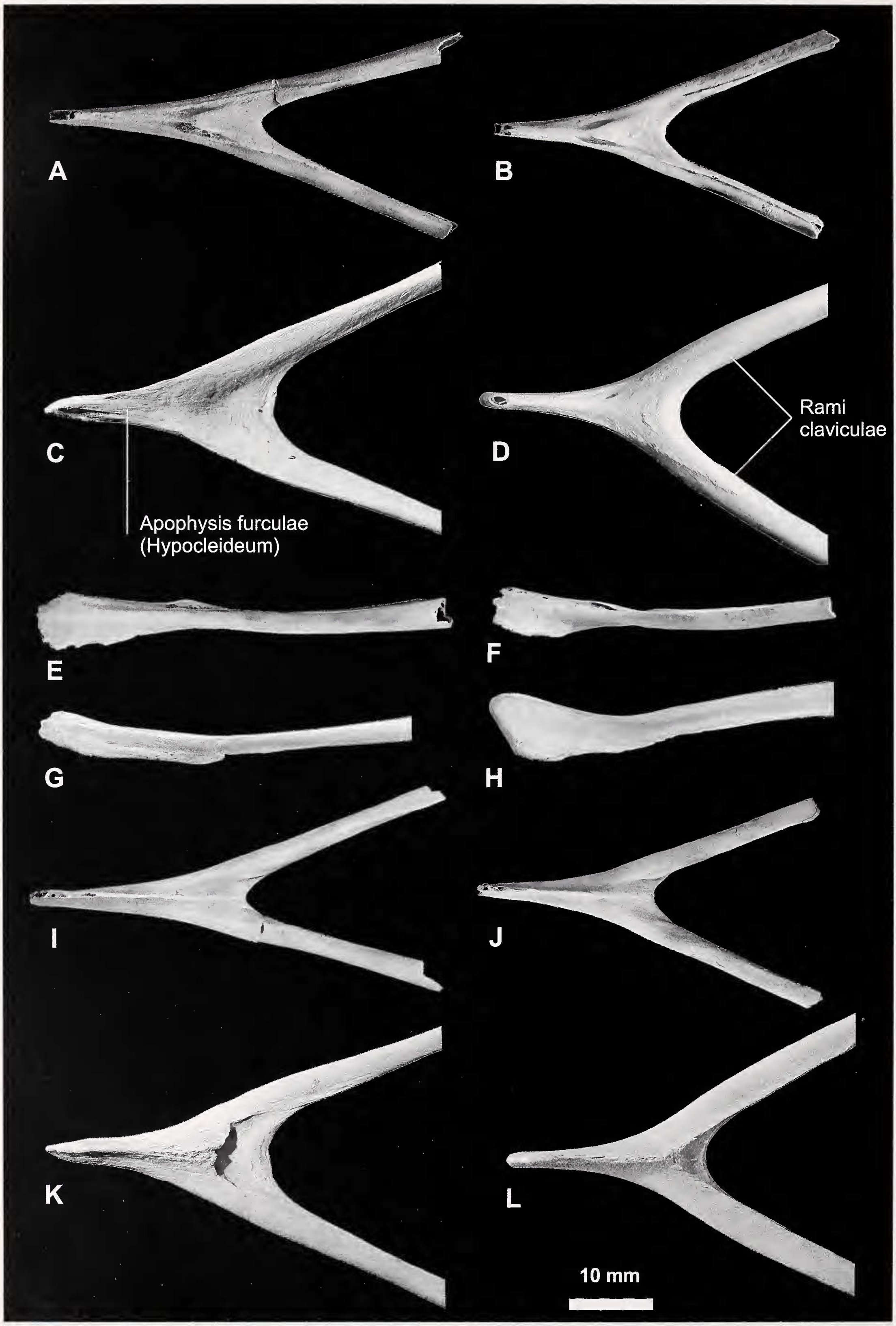


Figure 9 Furcula (sternal part) in anterior (A–D), lateral (E–H) and posterior (I–L) views. *Meleagris californica* (two specimens: A, E, and I; LACMHC J6536; B, F, and J; LACMHC J6546); *M. gallopavo* (C, G, and K; LACM 112167);

elongated Foramen rostri (rostral foramen) (character 2), a faint crest extending onto Rostrum sterni from Labrum ventrale (character 3), and the steep Spina dorsale rostri of the rostrum (character 4). *Meleagris ocellata* is distinguished from the other two species by the broadening posterior end (character 6) and an intermuscular line starting at the lateral tip of the Labrum ventrale (character 7).

CHARACTER 1. Lateral view.

State A (*M. ocellata*: 100%, N = 16; and *M. gallopavo*: 100%, N = 46): The Spina ventrale rostri (ventral spine) is a relatively large blade at the base of the Rostrum sterni. Its shape varies, and the transition between the ventral spine and the body of the rostrum can be sharp or gradual.

State B (*M. californica*: 100%, N = 11): The Spina ventrale rostri is a very small bump at the base of the body of the rostrum.

NB: The ventral spine of *M. ocellata*, as opposed to that of *M. gallopavo*, tends to connect gradually with the body of the rostrum, but individual variation within *M. ocellata* is too great to distinguish it as a separate state.

CHARACTER 2. Lateral view.

State A (*M. gallopavo*: 87%, N = 45): The Foramen rostri is elongated. Its upper, or dorsal, side looks narrow because it is partly screened by the Labrum dorsale.

State B (*M. ocellata*: 69%, N = 16; and *M. californica*: 98%, N = 41): The Foramen rostri is rounded or oval. It does not narrow much in its upper, or dorsal, side because it is screened little, if any, by the Labrum dorsale.

CHARACTER 3. Lateral view.

State A (*M. gallopavo*: 89%, N = 44): The crest, or anterior edge, of Labrum ventrale continues onto the Rostrum sterni as a faint and poorly visible line, but it reappears, usually as a broken line, in the more dorsal part of the body of the rostrum.

State B (*M. ocellata*: 94%, N = 16; and *M. californica*: 100%, N = 26): The crest, or anterior edge, of Labrum ventrale continues onto the Rostrum sterni as a high, sharp, and usually solid ridge that extends to the dorsal side of the body of the Rostrum sterni.

CHARACTER 4. Lateral view.

State A (*M. gallopavo*: 95%, N = 43): Dorsal edge of Spina dorsale rostri of Rostrum sterni curves sharply upward; it is clearly steeper, or more inclined, than the edge of the Labrum dorsale.

State B (*M. ocellata*: 93%, N = 15; and *M. californica*: 84%, N = 31): Dorsal edge of Spina dorsale rostri of Rostrum sterni is inclined approximately at the same angle as the edge of Labrum dorsale. The middle part of Spina dorsale rostri might bulge a little dorsad, but the general angle of inclination is smaller than in State A.

CHARACTER 5. Dorsal view [redefined from Howard (1927) and Steadman (1980)].

State A (*M. ocellata*: 94%, N = 16): Lateral edges of the Spina dorsale rostri are clearly convergent anteriad in dorsal view; the anterior part of Spina dorsale rostri is triangular, whereas its base is roughly rectangular.

State B (*M. gallopavo*: 71%, N = 45): Lateral edges of Spina dorsale rostri are less convergent anteriad and might bulge outward in the posterior portion. The size and shape of the dorsal rostral spine varies, but it is possible to distinguish an ill-defined triangular anterior and trapezoidal, or rounded, posterior section.

State C (*M. californica*: 94%, N = 31): Lateral edges of Spina dorsale rostri are convergent anteriad but straight or curving medially. The entire rostrum is triangular, and it is difficult to distinguish anterior and posterior sections.

NB: Strongly convergent lateral edges (State A) are observed exclusively in *M. ocellata*; atypical specimens of *M. gallopavo* show State C, or a combination of States B and C, but never State A.

CHARACTER 6. Dorsal view.

State A (*M. ocellata*: 76%, N = 17): The central portion of the sternum clearly broadens at its posterior end (Pars hepatica).

State B (*M. gallopavo*: 93%, N = 45; and *M. californica*: 100%, N = 3): The sternum either narrows gradually, or it broadens very slightly at its posterior end.

CHARACTER 7. Ventral view.

State A (*M. ocellata*: 94%, N = 17): Lineae intermusculares start at the lateral tips of Labrum ventrale.

State B (*M. gallopavo*: 94%, N = 48; and *M. californica*: 84%, N = 45): Lineae intermusculares start from the body of the sternum, lateral to the tips of Labrum ventrale.

NB: These intermuscular lines are continuous with those on the coracoid (character 8).

←

M. ocellata (D, H, and L; LACM 112170). The crest on the hypocleideum, which can be forked or straight, and with or without a "pocket," is species specific (character 3; views I–L). In *M. californica*, the intermuscular lines on the anterior side are easily seen (character 5; views A and B *vs.* C and D), and the triangular surface of the hypocleideum is bulging anteriad (character 6; views E and F *vs.* G and H). *Meleagris ocellata* has relatively robust rami, a character that is not readily seen in this figure (character 1; view L *vs.* I–K), its rami curve slightly outward (character 2; view L *vs.* I–K), and the rami are either straight or curve anteriad (character 4; view H *vs.* E–G).

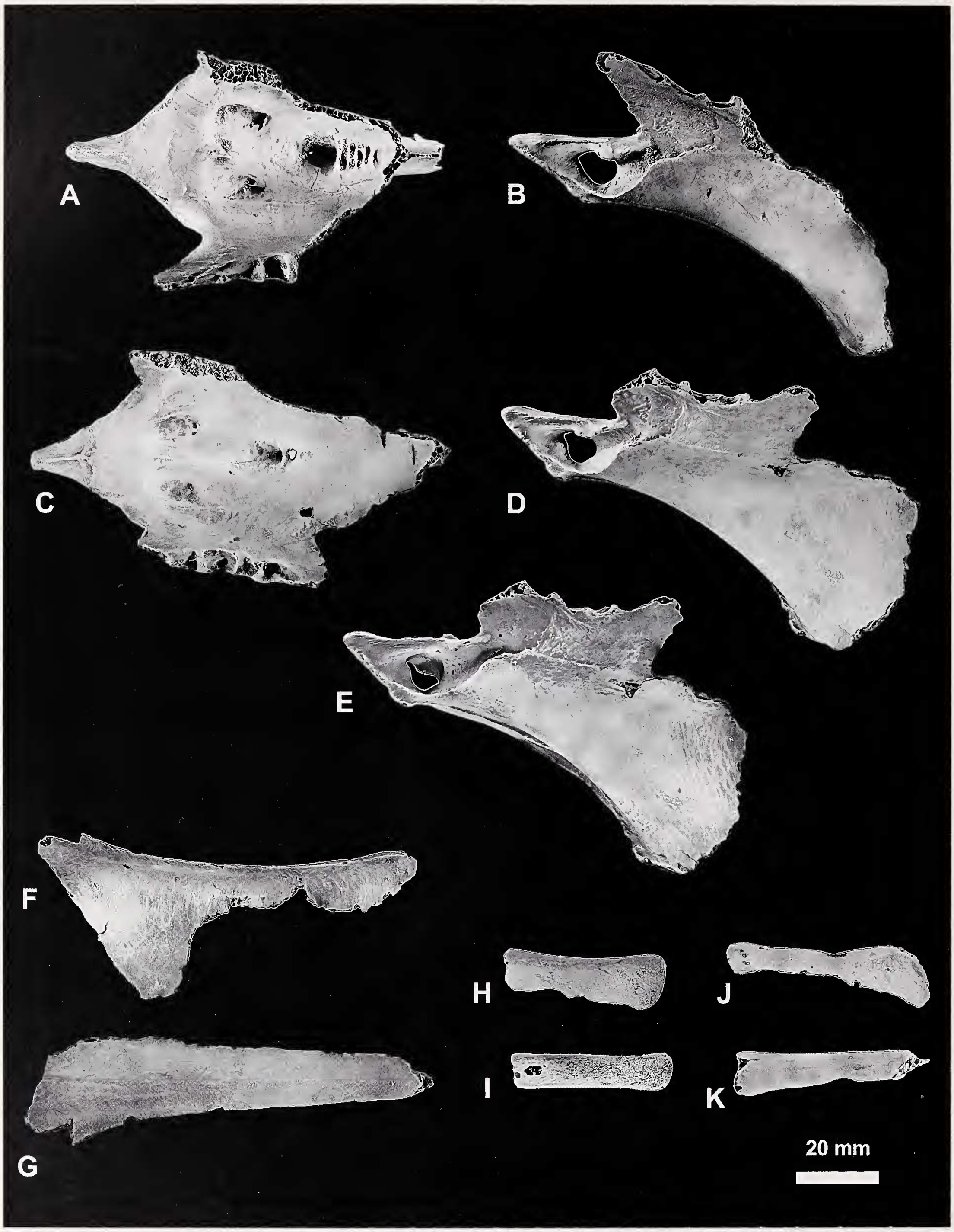


Figure 10a Sternum of *M. californica* in dorsal (**A**, **C**, **G**, **I**, and **K**), lateral (**B**, **D**, **F**, **H**, and **J**), and ventrolateral (**E**) views. Fragments **F–K** represent the central posterior portion (Pars hepatica), anterior to left. **A, B**; LACMHC C1393; **C, D, E**; LACMHC E5691; **F, G**; LACMHC C1069; **H, I**; LACMHC F2402; **J, K**; LACMHC F2430

CHARACTER 8. Relative width of sternum, expressed as ratio of measurements A and B.

State A (*M. ocellata*: 93%, N = 15): Sternum is relatively narrow; mean ratio of measurements A (width of Labrum ventrale) and B (distance between Labrum ventrale and Labrum dorsale) is 3.0 mm (2.55–3.29).

State B (*M. gallopavo*: 95%, N = 43): Sternum is relatively broad; mean ratio of measurements A:B is 3.7 (3.39–4.3).

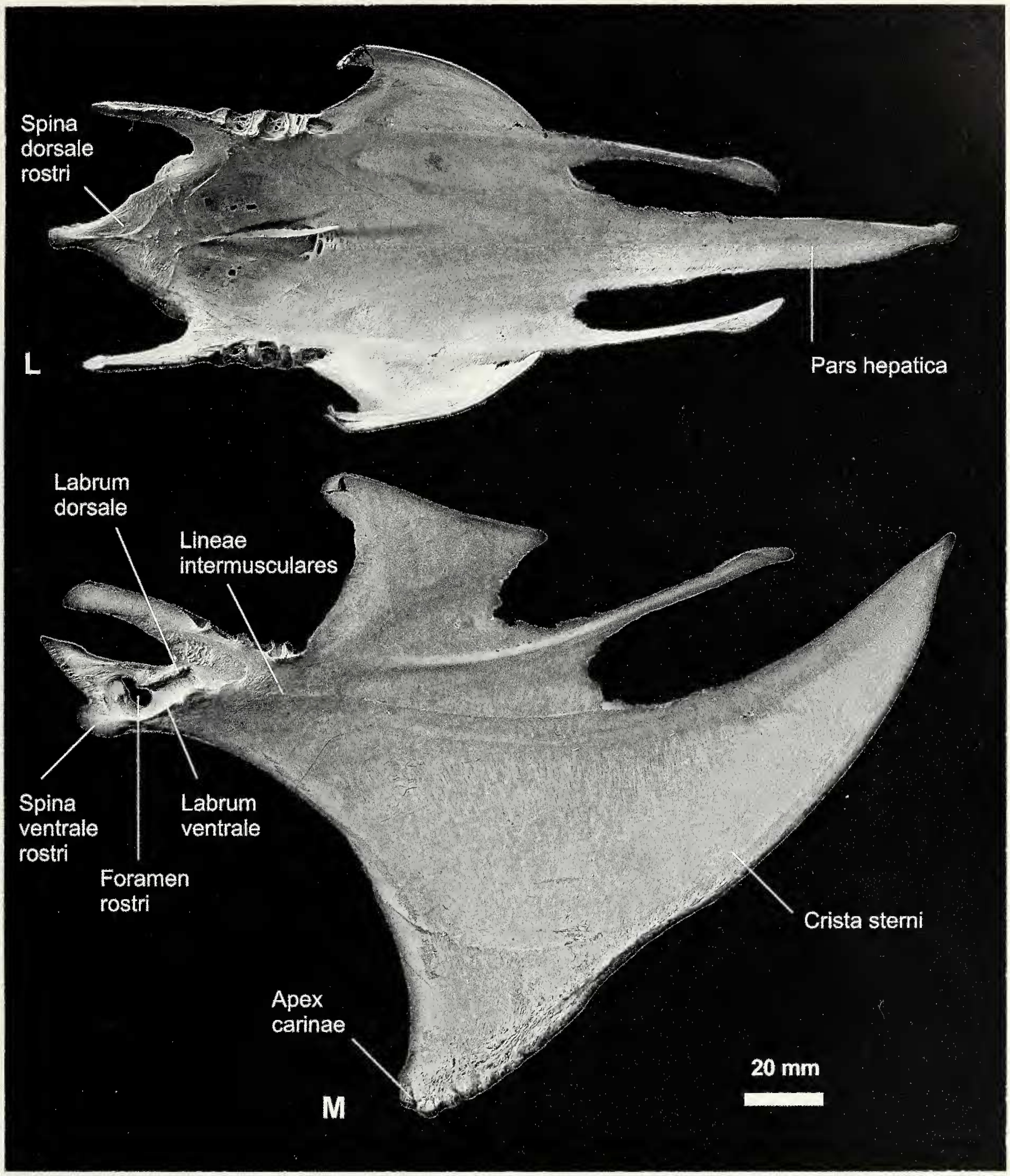


Figure 10b Sternum of *M. gallopavo* in dorsal and lateral views (L, M; LACM 112162)

NB: See Table A4 for measurements and Figure 11 for scatter diagram of measurements A and B. In *M. californica*, the ratio of measurements A:B is intermediate between those of the modern species. For the 56 specimens available, its mean value is 3.34 mm, with a range of 2.98–3.78 mm.

CORACOID

The coracoid is one of the best elements for differentiating the three species studied, with many reliable characters (Fig. 12). Most of the characters are located on the scapular portion; the sternal portion shows much individual variation, and it provided only one valid character. The following five characters are typical of *M. californica*: rounded Cotyla scapularis (character 2), gradual transition between Cotyla scapularis and Processus procoracoideus (character 3), blunt tip of Processus procoracoideus (character 4), thin Processus acrocoracoideus (character 5), and gradual ending of the Impressio lig. acrocoraco-

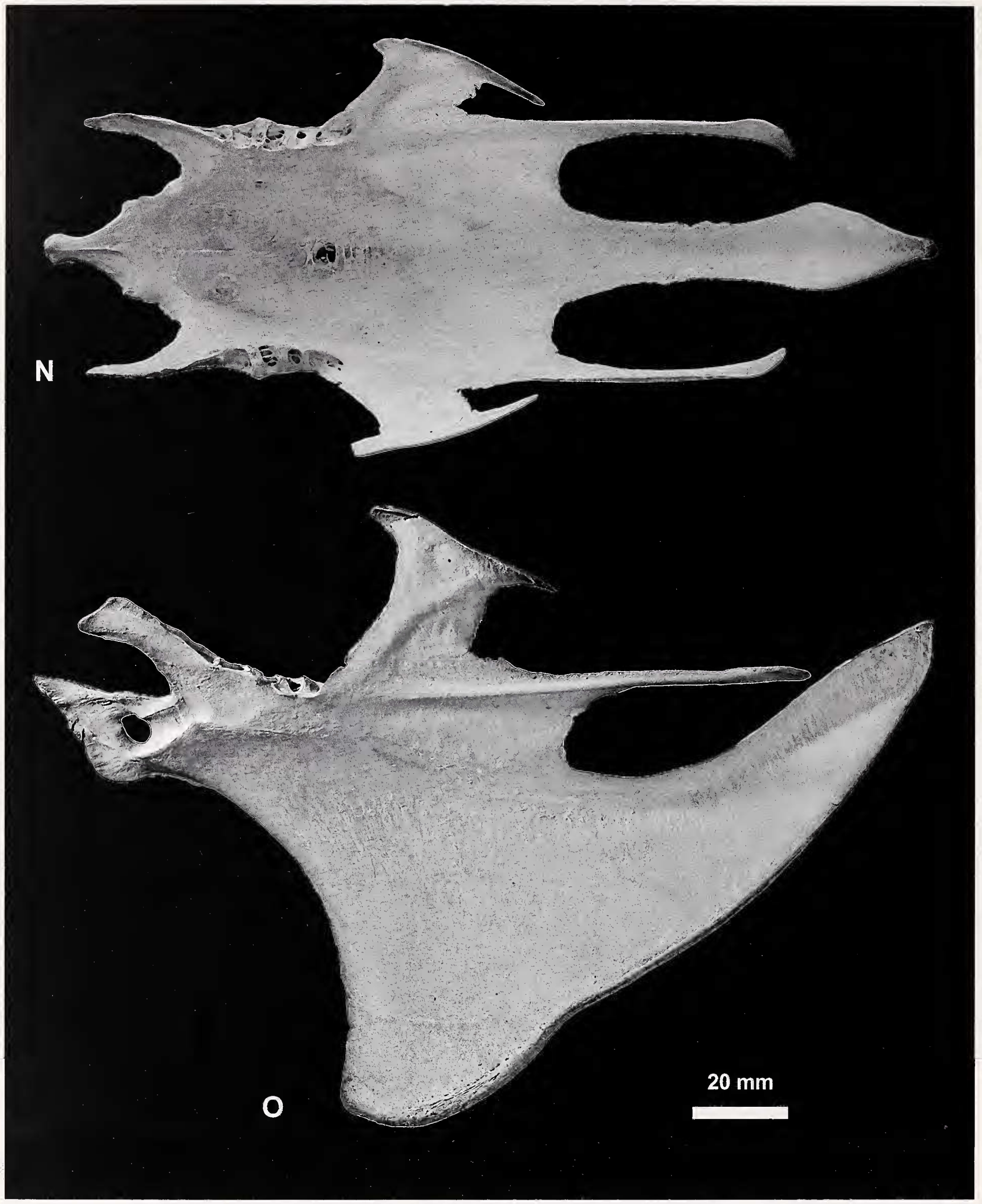


Figure 10c Sternum of *M. ocellata* in dorsal and lateral views (N, O; LACM 112170) The shape of the Spina dorsale rostri, in dorsal view, is species specific (character 5; views A, C *vs.* L *vs.* N). Typical of *M. californica* is a small Spina ventrale rostri on the Rostrum sterni (character 1; views B and D *vs.* M and O). Structures typical of *M. gallopavo* include the elongated Foramen rostri (rostral foramen) (character 2; views M *vs.* B, D, and O), faint crest extending onto Rostrum sterni from Labrum ventrale (character 3; views M *vs.* B, D, and O), and the steep Spina dorsale rostri of the rostrum (character 4; views M *vs.* B, D, and O). *Meleagris ocellata* is distinguished from the other two species by the broadening posterior end (Pars hepatica) (character 6; views N *vs.* I, K, and L), and an intermuscular line starting at the lateral tip of the Labrum ventrale (character 7; views O *vs.* E and M). The relative width of the sternum differs between *M. ocellata* and *M. gallopavo*, with *M. californica* being intermediate, but because this character can best be checked by comparing the ratio of measurements A and B (Fig. 11), the appropriate views are not shown (for details see character 8).

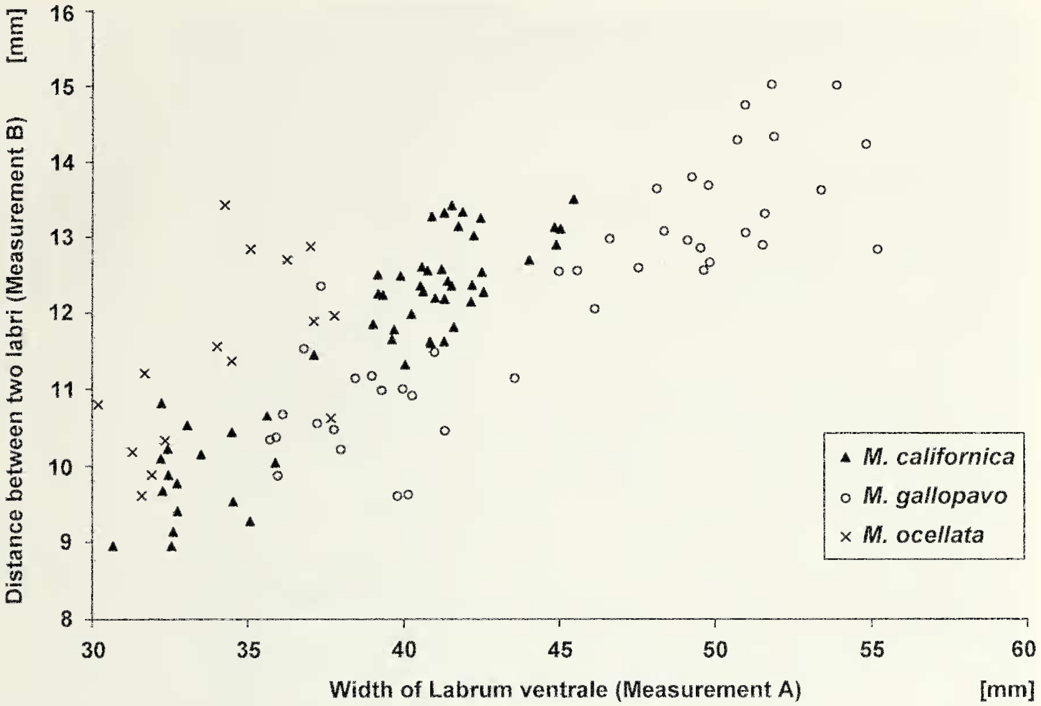


Figure 11 Sternum: Scatter diagram of measurements A and B (refers to sternum character 8, Table A4, and Fig. A2). In *M. ocellata*, the sternum is relatively narrower than in *M. gallopavo*, with *M. californica* being intermediate and overlapping the modern species. In this diagram it is possible to tell apart most specimens of *M. ocellata* from those of *M. gallopavo* (see also ratios described in character 8), as well as larger specimens of *M. gallopavo* from larger specimens of *M. californica*.

humeralis (character 7). Structures typical of *M. ocellata* include intermuscular line on posteromedial side of the shaft without any breaks (character 1), round Facies articularis clavicularis (character 6), and Linea intermuscularis ventralis ending at the Angulus lateralis (character 8).

CHARACTER 1. Shaft, posterior view [redefined from Howard (1927) and Steadman (1980)].

State A (*M. ocellata*: 94%, N = 18): Intermuscular line on posteromedial edge of shaft has no major breaks, and it marks the edge of the shaft (medial side of shaft is not visible or only slightly visible).

State B (*M. gallopavo*: 96%, N = 49; and *M. californica*: 81%, N = 59): There is at least one gap in the posteromedial intermuscular line, which usually, but not always, curves laterad inside the edge of the shaft to various degrees. The medial side of shaft is partially visible. The gap seems to be larger in *M. g. osceola* and *M. g. silvestris* and smaller in *M. g. intermedia* and *M. g. merriami*, but this observation might also be a result of coincidence. We did not have enough specimens to prove it one way or the other.

CHARACTER 2. Scapular part, posterior view [see Howard (1927) and Steadman (1980)].

State A (*M. ocellata*: 88%, N = 17; and *M. gallopavo*: 94%, N = 50): The Cotyla scapularis is elongated.

State B (*M. californica*: 75%, N = 91): The Cotyla scapularis is more rounded.

CHARACTER 3. Scapular part, posterior and medial views.

State A (*M. ocellata*: 88%, N = 17; and *M. gallopavo*: 82%, N = 50): Transition between Cotyla scapularis and Processus procoracoideus is sharp because the sternal margin of Cotyla scapularis is raised above the shaft surface.

State B (*M. californica*: 91%, N = 90): Transition between Cotyla scapularis and Processus procoracoideus is gradual because the sternal margin of Cotyla scapularis is raised only slightly above the shaft surface.

CHARACTER 4. Scapular part, posterior and medial views [redefined from Martin and Tate (1970); see also Steadman (1980)].

State A (*M. ocellata*: 94%, N = 18; and *M. gallopavo*: 80%, N = 50): In posterior view, medial end of Processus procoracoideus is sharper, and in medial view it is more rounded.

State B (*M. californica*: 69%, N = 91): In posterior view, medial end of Processus procoracoideus is more blunt, and in medial view it is often elongated.

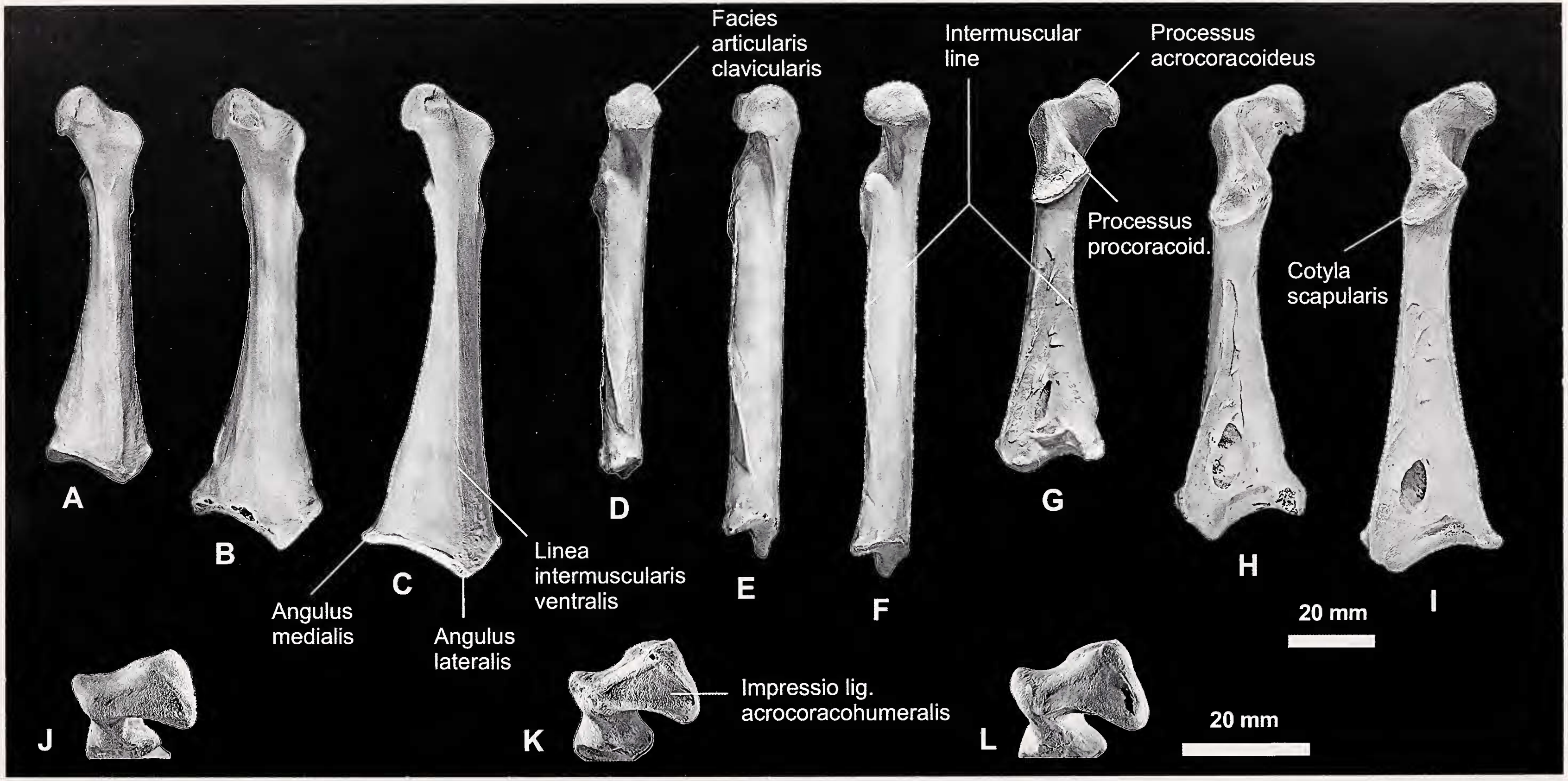


Figure 12 Left coracoid in anterior (A–C), medial (D–F), posterior (G–I), and scapular (J–L) views. *Meleagris californica* (B, E, H, and K; LACMHC E7239); *M. gallopavo* (C, F, I, and L; LACM 112165); *M. ocellata* (A, D, G, and J; UMMZ 151342). In *M. californica*, the Cotyla scapularis is rounded (character 2; view H *vs.* G and I), the transition between Cotyla scapularis and Processus procoracoideus is gradual (character 3; views E, H *vs.* D, G and F, I), the tip of Processus procoracoideus is blunt (character 4; views E, H *vs.* D, G and F, I), the Processus acrocoracoideus is thin (character 5; view H *vs.* G and I), and the medial ending of the Impressio lig. acrocoracohumeralis is gradual (character 7; view K *vs.* J and L). *Meleagris ocellata* has an intermuscular line on medial side of the shaft without any breaks (character 1; view G *vs.* H and I), a round Facies articularis clavicularis (character 6; view D *vs.* E and F), and a Linea intermuscularis ventralis ending at the Angulus lateralis (character 8; view A *vs.* B and C).

CHARACTER 5. Scapular part, posterior view.

State A (*M. ocellata*: 65%, N = 17; and *M. gallopavo*: 88%, N = 50): Mediosternal end of Processus acrocoracoideus is broad and massive.

State B (*M. californica*: 91%, N = 68): Mediosternal end of Processus acrocoracoideus is narrow and delicate.

CHARACTER 6. Scapular part, medial view [Howard (1927); see also Steadman (1980)].

State A (*M. ocellata*: 71%, N = 17): Facies articularis clavicularis is round.

State B (*M. gallopavo*: 94%, N = 50; and *M. californica*: 92%, N = 93): Facies articularis clavicularis is oval.

CHARACTER 7. Scapular part, scapular view [redefined from Howard (1927); see also Steadman (1980)].

State A (*M. ocellata*: 100%, N = 17; and *M. gallopavo*: 84%, N = 50): Medial edge of Impressio lig. acrocoracohumeralis ends abruptly with a crest on the top of the bone.

State B (*M. californica*: 88%, N = 101): Medial edge of the Impressio lig. acrocoracohumeralis ends gradually on the medial side of the bone; there is no bony crest.

CHARACTER 8. Sternal part, anterior view.

State A (*M. ocellata*: 87%, N = 16): Linea intermuscularis ventralis ends at Angulus lateralis, or even medial to it.

State B (*M. gallopavo*: 85%, N = 47; and *M. californica*: 80%, N = 81): Linea intermuscularis ventralis curves laterally and ends clearly lateral to Angulus lateralis.

NB: The intermuscular lines match as continuations of those on the sternum, character 7.

SCAPULA

The scapula provided only one valid character, which was the nature of the intermuscular line extending posteriad from the Tuberculum m. scapulotricipitis (Fig. 13). It distinguishes *M. ocellata* from the other two taxa.

CHARACTER 1. Shaft, medial and ventrolateral views.

State A (*M. ocellata*: 72%, N = 18): Relatively sharp edge curves distad from Tuberculum m. scapulotricipitis along the medial side to about midlength of the blade. In ventrolateral view, the edge forms ventromedial border of the bone.

State B (*M. gallopavo*: 86%, N = 50; and *M. californica*: 100%, N = 80): In ventrolateral view, muscle line goes from Tuberculum m. scapulotricipitis to the medial side of the bone, where it curves deeply dorsomediad or vanishes and reappears farther distally.

HUMERUS

The combination of characters of the humerus distinguishes all three species, provided that the bone is complete (Fig. 14). Typical of *M. californica* is a deep Fossa pneumatica (character 1), whereas structures typical of *M. ocellata* include an anterodorsal position of the attachment of the Ligamentum humeroulnare anterior (character 2), the anterior position of the attachment of M. pronator superficialis (character 3), and a relatively greater depth of the Condylus dorsalis (character 4).

CHARACTER 1. Proximal part, posterodistal view.

State A (*M. ocellata*: 94%, N = 16; and *M. gallopavo*: 73%, N = 48): Fossa pneumatica next to Crista bicipitalis is shallow.

State B (*M. californica*: 93%, N = 82): Fossa pneumatica next to Crista bicipitalis is deep.

CHARACTER 2. Distal part, anterior view.

State A (*M. ocellata*: 76%, N = 17): The attachment of Lig. humeroulnare anterior faces anterodorsad.

State B (*M. gallopavo*: 100%, N = 48; and *M. californica*: 100%, N = 52): The attachment of Lig. humeroulnare anterior faces anteriad.

CHARACTER 3. Distal part, anterior view [see Howard (1927) and Steadman (1980)].

State A (*M. ocellata*: 76%, N = 17): Attachment of M. pronator superficialis faces more anteriad.

State B (*M. gallopavo*: 90%, N = 48; and *M. californica*: 88%, N = 51): Attachment of M. pronator superficialis faces more ventrad.

CHARACTER 4. Relative depth of Condylus dorsalis, expressed as ratio of measurements A (total length) and G (depth of Condylus dorsalis).

State A (*M. ocellata*: 73%, N = 15): The depth of Condylus dorsalis is relatively large; the ratio of measurements A:G is ≤ 8.6 (mean: 8.45; range: 8.19–8.56).

State B (*M. gallopavo*: 84%, N = 44; and *M. californica*: 96%, N = 94): The depth of Condylus dorsalis is relatively small; the ratio of measurements A:G is ≥ 8.69 (mean: 9.0; range: 8.69–9.75).

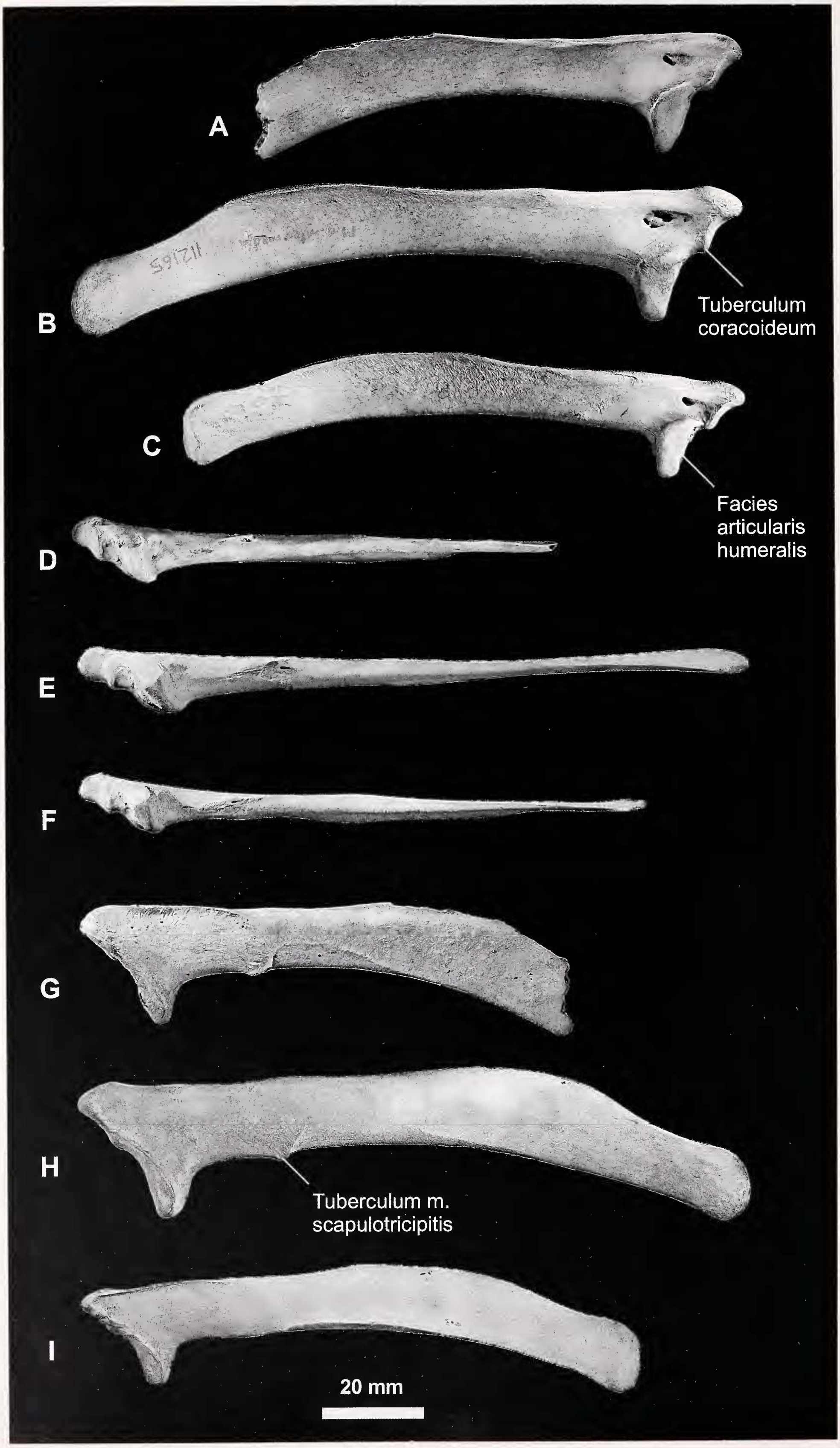
NB: See Table A7 for measurements and Figure 15 for scatter diagram of measurements A and G.

ULNA

Usually, the two characters found on the ulna allow all three species to be distinguished (Fig. 16), yet the species-specific character 1, shape of attachment of M. brachialis, is not perfect (see percentages of typical specimens), and therefore it might not always be possible to identify a specimen correctly. Typical of *M. ocellata* are larger differences between the minimum and maximum diameters at the midshaft (character 2).

CHARACTER 1. Proximal part, ventral view.

State A (*M. gallopavo*: 88%, N = 48): Attachment of M. brachialis is broad throughout


A
B
Tuberculum coracoideum
C
Facies articularis humeralis
D
E
F
G
H
Tuberculum m. scapulotricipitis
I
20 mm

most of its length. It is almost flat in the anteroposterior axis.

State B (*M. ocellata*: 65%, N = 17): Attachment of M. brachialis is long and narrower than in State A. Its distal end usually tapers, the midpart is broad, and the proximal part is narrower than the distal. It is almost flat in the anteroposterior axis.

State C (*M. californica*: 68%, N = 87): Attachment of M. brachialis is long and narrow throughout its length. In about half the specimens the attachment is slanting, with its posterior edge being clearly raised.

NB: In *M. californica*, 50 percent of specimens have the surface of, and surrounding, the actual attachment area of M. brachialis smooth, probably as a result of pit wear, young age, or both. Therefore, it is not possible to determine the exact size or shape of the attachment area, which makes it impossible to assign them to any category. In such cases, the additional criterion of a sloping versus flat surface of attachment can be used because the great majority of both extant taxa have a flat surface of attachment (*M. ocellata*: 100%; *M. gallopavo*: 88%), whereas in *M. californica* it is sloping in 50 percent of the individuals.

CHARACTER 2. Relative diameters at midshaft, expressed as ratio of measurement E (minimum diameter at midshaft) and F (maximum diameter at midshaft).

State A (*M. ocellata*: 88%, N = 17): Differences between minimum and maximum diameters at midshaft are larger than in State B; the ratio of measurements E:F is ≤ 0.75 (mean: 0.72; range: 0.69–0.75).

State B (*M. gallopavo*: 91%, N = 43; and *M. californica*: 98%, N = 223): Differences between minimum and maximum diameters at midshaft are smaller than in State A; the ratio of measurements E:F is ≥ 0.77 (mean: 0.81; range: 0.77–0.87).

NB: See Table A8 for measurements and Figure 17 for scatter diagram of measurements E and F.

RADIUS

The combination of three characters of the radius allows all three species to be distinguished if the bone is complete or, if at least its distal end is well preserved (Fig. 18). Typical of *M. californica* is the curving dorsal edge of Facies articularis radiocarpalis (character 3), whereas structures typical of *M. ocellata* include a more pronounced rotation of the proximal and distal ends (characters 1 and 2, respectively). Characters 1 and 2 are connected with each other; they refer to the rotation, or bending, of articular ends in opposite directions such that the shaft of the radius remains parallel to that of the ulna. As a result, the radius and ulna are probably slightly farther away from each other in *M. ocellata* than in *M. gallopavo* and *M. californica*.

CHARACTER 1. Proximal part, anterior view.

State A (*M. ocellata*: 87%, N = 15): Proximal end rotated anteroventrad, which results in (a) Facies articularis ulnaris being at an angle to the long axis of the bone, and (b) a clear slanting of the Cotyla humeralis.

State B (*M. gallopavo*: 72%, N = 46; and *M. californica*: 91%, N = 77): Proximal end little rotated anteroventrad, which results in (a) Facies articularis ulnaris being almost parallel to the long axis of the bone, and (b) little slanting of the Cotyla humeralis.

NB: Both aspects resulting from this character (i.e., slanting of the Facies articularis ulnaris and the Cotyla humeralis) are equally important.

CHARACTER 2. Distal part, posterior view.

State A (*M. ocellata* 75%, N = 16): Distal end rotated posteriad more than in State B, which results in (a) steep transition between the shaft and the midpart of Facies articularis radiocarpalis, and (b) a larger and more visible ridge at the anterior end of the Facies articularis radiocarpalis.

State B (*M. gallopavo*: 77%, N = 47; and *M. californica*: 75%, N = 120): Distal end little rotated posteriad, which results in (a) gradual transition between the shaft and the midpart of Facies articularis radiocarpalis, and (b) little or no ridge at the anterior end of the Facies articularis radiocarpalis.

NB: In this case, the former aspect of the character (i.e., a steep vs. gradual transition) is more important than the latter.

CHARACTER 3. Distal part, posterior, dorsal, and anterior views [redefined from Howard (1927) and Steadman (1980)].

State A (*M. ocellata*: 80%, N = 15; and *M. gallopavo*: 94%, N = 47): Dorsal edge of Facies articularis radiocarpalis gradually merges with the shaft. In posterior view the dorsal edge is visible, and in dorsal and anterior views one can see that its proximal end does not curve into the anterior side of the radius.

State B (*M. californica*: 69%, N = 84): Dorsal edge of Facies articularis radiocarpalis is an

←

Figure 13 Right scapula in lateral (A–C), ventrolateral (D–F), and medial (G–I) views. *Meleagris californica* (A, D, and G; LACMHC E5445); *Meleagris gallopavo* (B, E, and H; LACM 112165); *M. ocellata* (C, F, and I; LACM 89958). In *M. ocellata*, the intermuscular line going from the Tuberculum m. scapulotricipitis forms the medial border of the bone (in ventrolateral view), whereas in the other two species it curves to the medial side of the bone (view F and I *vs.* D–E and G–H).

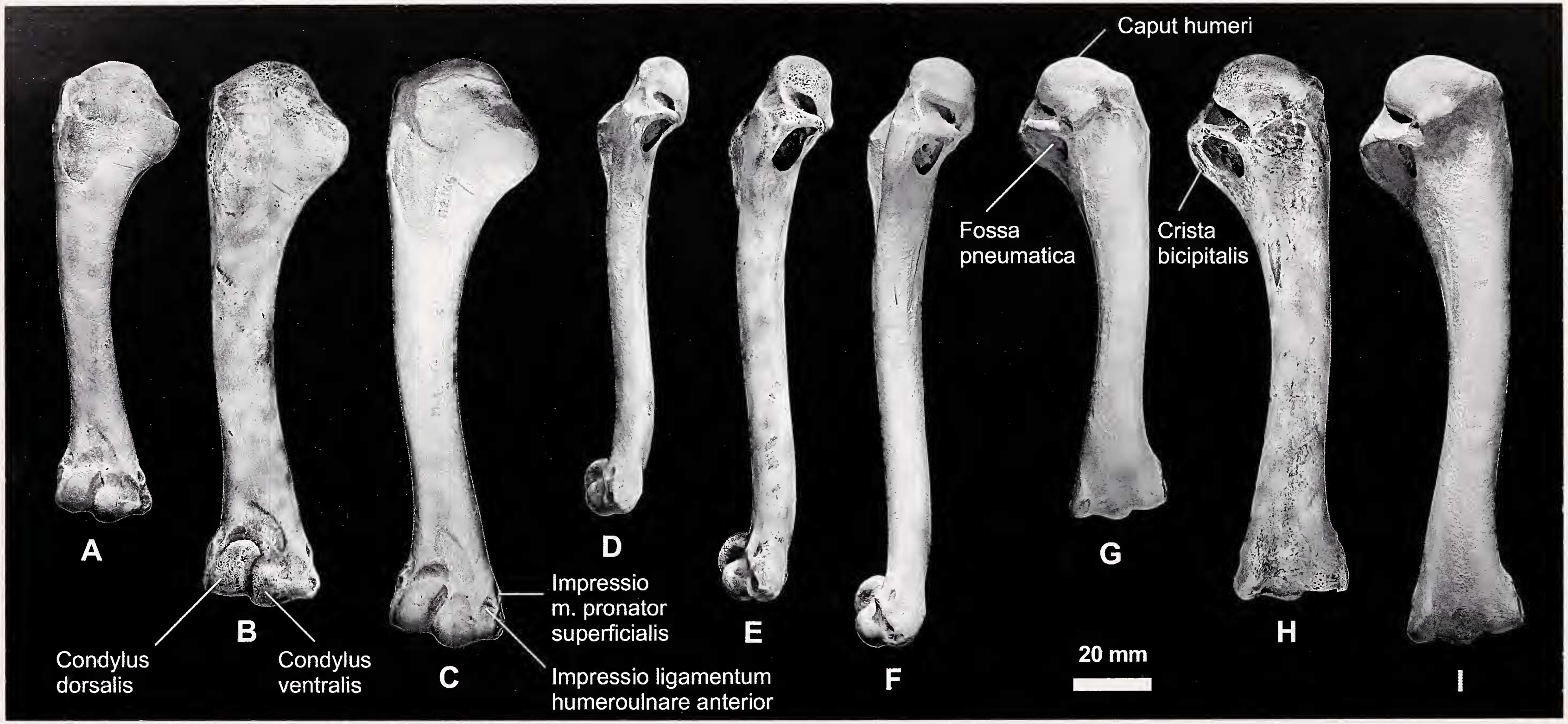


Figure 14 Right humerus in anterior (A–C), ventral (D–F), and posterior (G–I) views. *Meleagris californica* (B, E, and H; LACMHC E5755); *M. gallopavo* (C, F, and I; LACM 112166); *M. ocellata* (A, D, and G; LACM 106510). Typical of *M. californica* is a deep Fossa pneumatica (character 1; view H *vs.* G and I). In *M. ocellata*, the attachment of the Ligamentum humeroulnare anterior faces anterodorsad (character 2; view A *vs.* B and C), the attachment of M. pronator superficialis faces more anteriad (character 3; view A *vs.* B and C), and the depth of the Condylus dorsalis is large relative to the total length of the bone, which can best be checked by comparing the ratio of measurements A and G (character 4; Fig. 15).

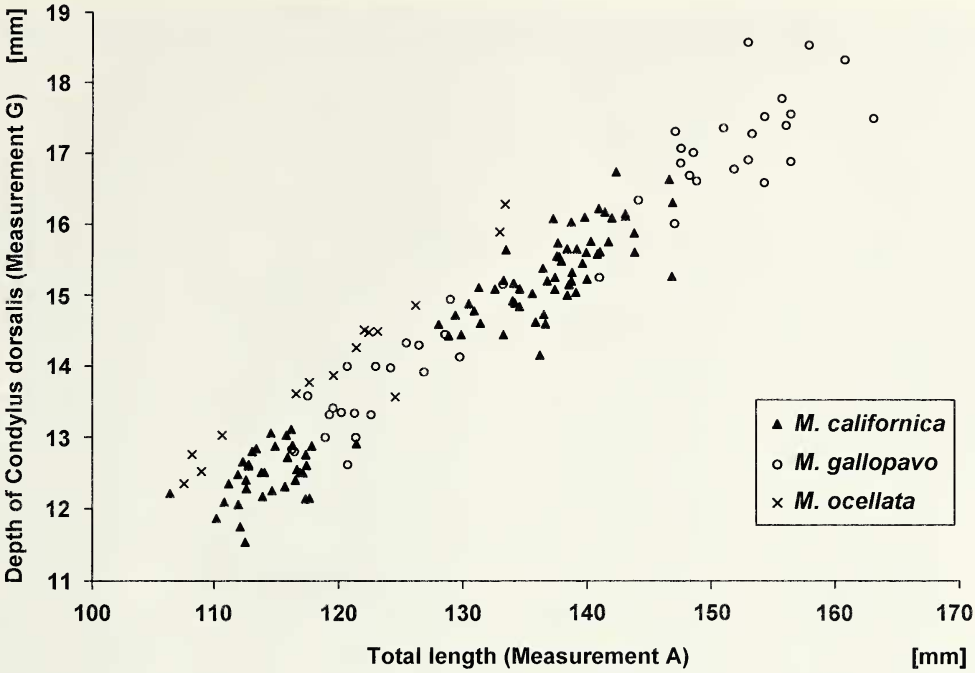


Figure 15 Humerus: Scatter diagram of measurements A and G (refers to humerus character 4, Table A7, and Fig. A3). In *M. ocellata*, the depth of the Condylus dorsalis is relatively greater than that in *M. gallopavo* and *M. californica*. The difference is not large, but it is clear. Moreover, sexual size dimorphism in *M. gallopavo* and *M. californica* allows reliable identification in many cases. The gap between males and females of *M. gallopavo* is filled in by males of *M. californica*, whereas most females of *M. californica* are smaller than females of *M. gallopavo*. The overlapping zones are not very large, and only a few specimens are clearly outside their categories. For example, only two specimens of *M. gallopavo* were found in the zone typical of male *M. californica* (total length between 130 and 144 mm), and no specimens of *M. gallopavo* had a total length smaller than 116 mm.

independent structure, easily distinguished from the shaft edge. In posterior view, the proximal end of the dorsal edge is hidden behind the shaft edge, and in dorsal and anterior views the dorsal edge curves into the anterior side of the radius.

CARPOMETACARPUS

The carpometacarpus is not a very good element for distinguishing the three species of turkeys (Fig. 19). Typical of *M. ocellata* is a very shallow notch in the ventral rim of the Trochlea carpalis (character 1). Certain specimens of *M. gallopavo* can be distinguished from those of *M. californica* by the proximal width of the bone and the ratio of measurements C and F (character 2), but because of an extensive overlap zone, the usefulness of this character is rather limited.

CHARACTER 1. Proximal part, ventral and articular views [redefined from Brodkorb (1964b) and Steadman (1980)].

State A (*M. ocellata*: 84%, N = 19): Notch in the ventral rim of Trochlea carpalis is very shallow and broad. In articular view, the ventral rim of the trochlea continues through the notch.

State B (*M. gallopavo*: 100%, N = 46): Notch in the ventral rim of Trochlea carpalis is deep and broad or very deep and narrow. In articular view, the ventral rim of the trochlea is broken by the notch.

NB: Specimens of *M. californica* are divided almost evenly between the two states (State A = 46%, State B = 54%; N = 270), but the character is very stable in extant taxa.

CHARACTER 2. Combination of (a) absolute value of measurement C (proximal width) and (b) ratio of measurement C and F (midwidth).

State A (*M. gallopavo*: 71%, N = 45): Proximal width (measurement C) greater than 23 mm, or its value is between 17 and 23 mm, and the ratio C:F is ≥ 1.3.

State B (*M. californica*: 56%, N = 222): Proximal width (measurement C) smaller than 17 mm, or its value is between 17 and 23 mm, and the ratio C:F is ≤ 1.2.

NB: See Table A10 for measurements and Figure 20 for scatter diagram of measurements C and F. *Meleagris ocellata* cannot be distinguished from the other two species by this character because

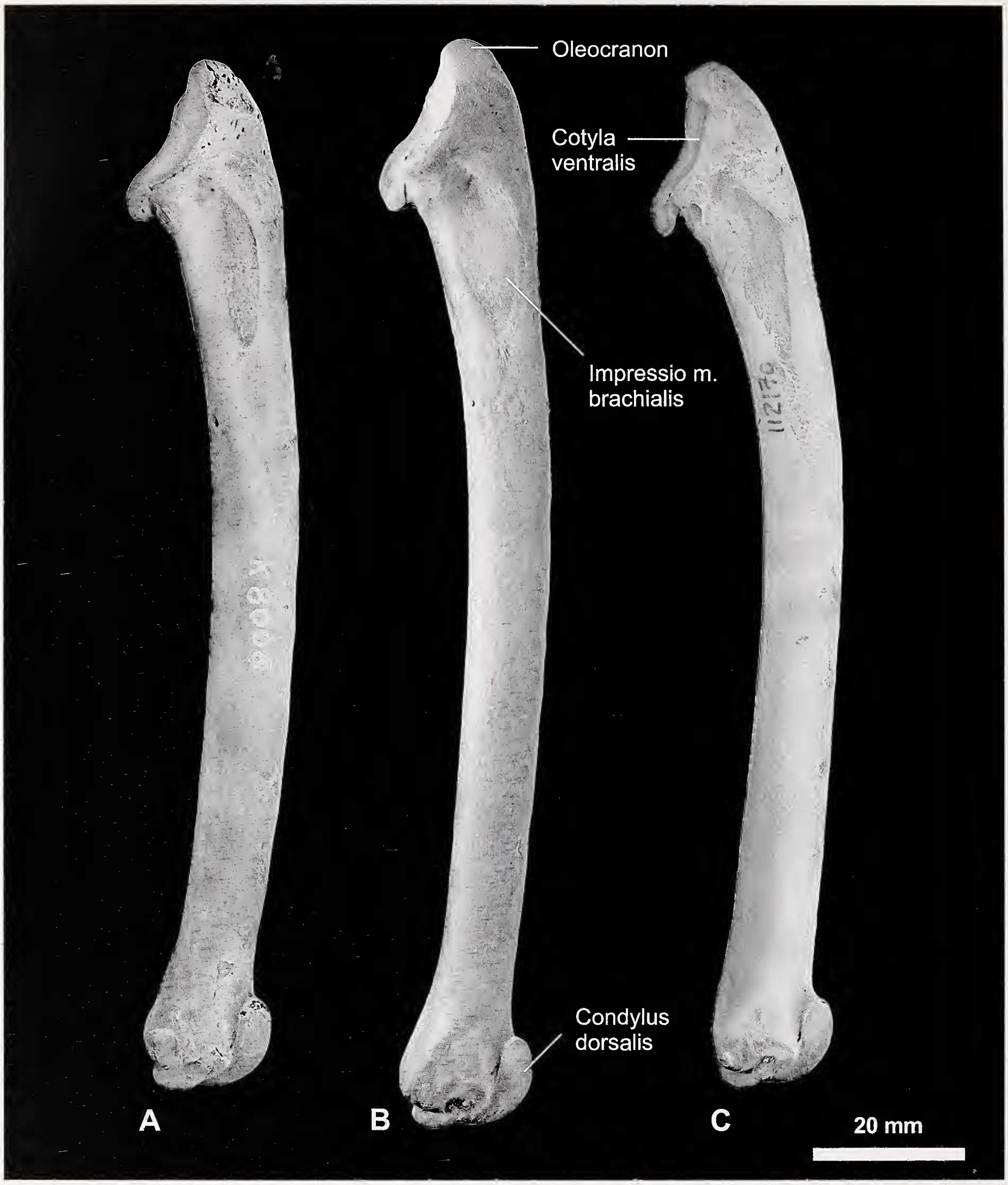


Figure 16 Right ulna in ventral view. *Meleagris californica* (**A**, LACMHC K8006); *M. gallopavo* (**B**, LACM 112431); *M. ocellata* (**C**, LACM 112170). The shape of attachment of M. brachialis is species specific, although there are a number of atypical forms, especially in *M. ocellata* and *M. californica* (character 1; view **A** *vs*. **B** *vs*. **C**). In *M. ocellata*, the differences between the minimum and maximum diameters at the midshaft are larger than in the other two species, but this character can best be checked by comparing the ratio of measurements E and F (character 2; Fig. 17).

---

it is intermediate in size and form; thus, it can be eliminated only on the basis of its geographical distribution. The large overlap between *M. gallopavo* and *M. californica* results in the low percentages of "typical" specimens. Nevertheless, if a specimen to be identified falls into one of the "typical" categories (i.e., not into the overlapping zone), the identification is reliable. No specimens of *M. californica* with measurement C larger than 23 mm or of *M. gallopavo* smaller than 17 mm were observed. However, there were a few exceptions in the ratio C:F for specimens whose

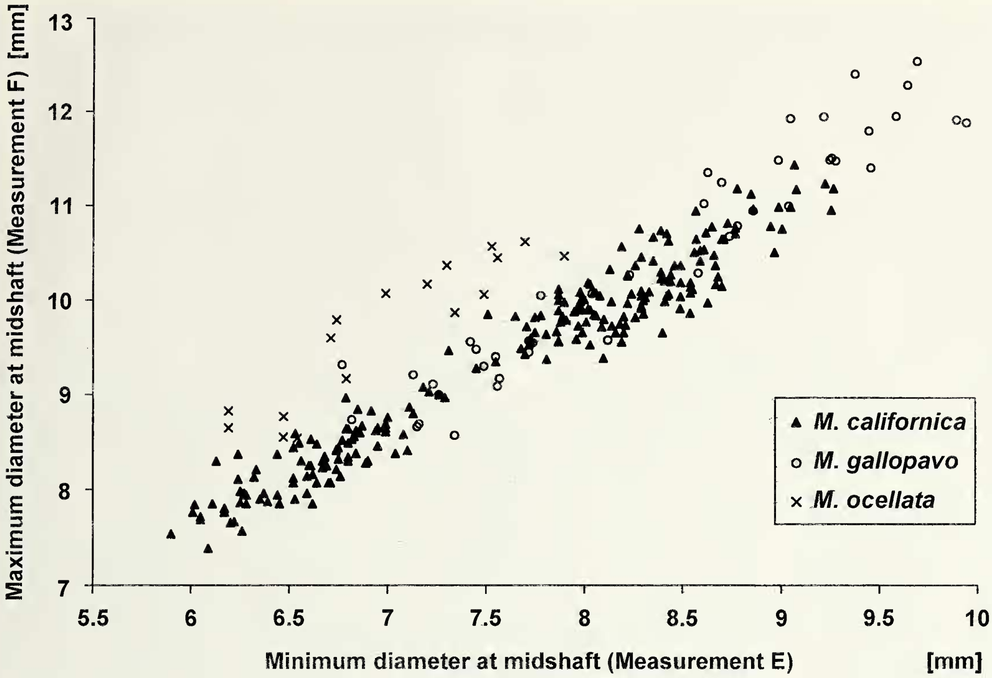


Figure 17 Ulna: Scatter diagram of measurements E and F (refers to ulna character 2, Table A8, and Fig. A4). In *M. ocellata*, the maximum diameter at midshaft is relatively greater than that in *M. gallopavo* and *M. californica*. The difference is not great, but it is clear.

measurement C ranged between 17 and 23 mm (three specimens of *M. californica* in State A and two specimens of *M. gallopavo* in State B).

PHALANX PROXIMALIS DIGITI MAJORIS

Two characters of the Phalanx proximalis digiti majoris distinguish *M. ocellata* from the other two species (Fig. 21). However, *M. californica* and *M. gallopavo* cannot be told apart using these characters. Distinguishing the latter two species is possible only by their measurements in certain conditions (e.g., large specimens of *M. gallopavo* are outside the range size of *M. californica*; see Table A11 for measurements).

CHARACTER 1. Ventral view.

State A (*M. ocellata*: 78%, N = 18): Proximal edge of Fossa ventralis is steep and well defined.

State B (*M. gallopavo*: 87%, N = 46; and *M. californica*: 67%, N = 108): There is a gradual transition between Fossa ventralis and proximal part of the phalanx.

CHARACTER 2. Ventral view.

State A (*M. ocellata* 81%, N = 16): Proximal part of posterior edge is straight, curves gently outward, or curves only slightly and gently inward.

State B (*M. gallopavo*: 76%, N = 46; and *M. californica*: 91%, N = 112): Proximal part of posterior edge curves inward.

FEMUR

The only valid character on the femur, that is, a lesser trochanter with or without a transverse groove (Fig. 22), distinguishes *M. ocellata* from the other two species.

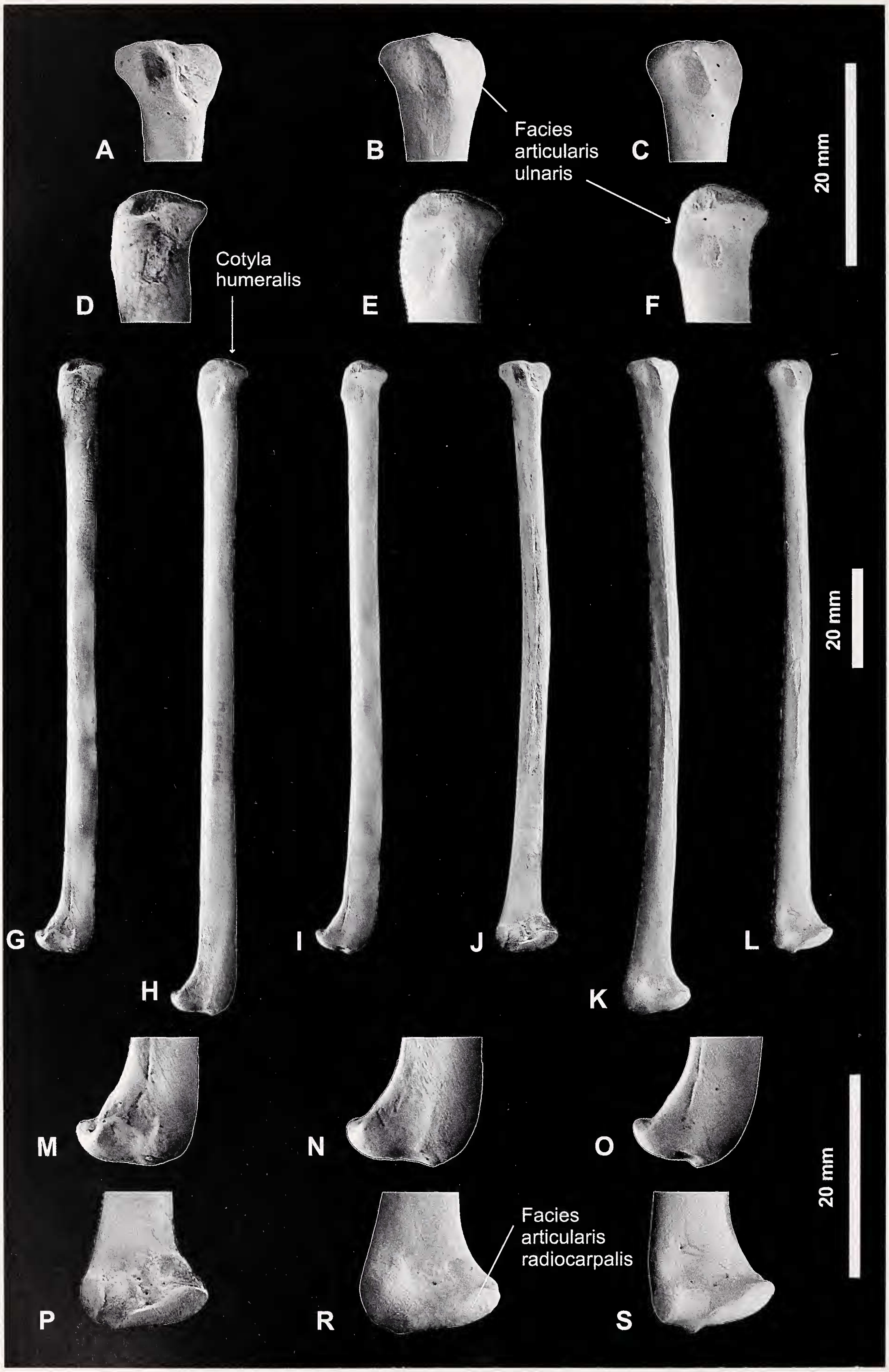
CHARACTER 1. Proximal part, posterior view [redefined from Howard (1927); see also Brodkorb (1964b) and Steadman (1980)].

State A (*M. ocellata*: 75%, N = 16): Lesser trochanter is not grooved, or it has only a very shallow transverse depression.

State B (*M. gallopavo*: 92%, N = 48; and *M. californica*: 79%, N = 92): Lesser trochanter has a transverse groove of various depth, which divides it into two protuberances (upper and lower).

TIBIOTARSUS

The combination of characters on the tibiotarsus should be sufficient to distinguish all three species provided that the bone is complete and well preserved (Fig. 23). Unfortunately, this seldom happens with tibiotarsi. Typical of *M. ocellata* is a bent Crista cnemialis cranialis (character 2), whereas structures typical of *M. californica* include a narrow Crista cnemialis cranialis (character 1) and a small, slightly protruding knob on the distal end (character 3).


A
B
Facies articularis ulnaris
C
20 mm
D
Cotyla humeralis
E
F
G
H
I
J
K
L
20 mm
M
N
O
20 mm
P
R
Facies articularis radiocarpalis
S

CHARACTER 1. Proximal part, medial view.

State A (*M. ocellata*: 81%, N = 16; and *M. gallopavo*: 75%, N = 40): Crista cnemialis cranialis is broad.

State B (*M. californica*: 74%, N = 80): Crista cnemialis cranialis is relatively narrow.

CHARACTER 2. Proximal part, anterior view [redefined from Howard (1927); see also Steadman 1980)].

State A (*M. ocellata*: 87%, N = 16): Anterior edge of Crista cnemialis cranialis clearly bends, or curves, laterad along most of its length.

State B (*M. gallopavo*: 100%, N = 48; and *M. californica*: 100%, N = 81): Crista cnemialis cranialis does not bend, or curve, laterad, or bends very little and then only at its proximal end.

CHARACTER 3. Distal part, lateral view.

State A (*M. ocellata*: 69%, N = 16; and *M. gallopavo*: 85%, N = 46): Knob in the middle of Condylus lateralis is larger and protrudes farther laterad than in State B.

State B (*M. californica*: 77%, N = 246): Knob is small, almost flat. It projects only slightly laterad.

FIBULA

The only valid character on the fibula, which is a bulging or flattened lateral surface of the proximal part (Fig. 24), distinguishes most specimens of *M. californica* from the other two species.

CHARACTER 1. Proximal part, lateral view [see Howard (1927) and Steadman (1980)].

State A (*M. ocellata*: 94%, N = 16; and *M. gallopavo*: 77%, N = 47): Middle part of proximal end is flattened or has only a slight bulge.

State B (*M. californica*: 70%, N = 99): Middle part of proximal end is bulging.

TARSOMETATARSUS

A combination of characters on the tarsometatarsus might be used to distinguish all three species of turkeys when the bone is complete and especially when it belongs to an adult male with a fully developed spur (Fig. 25). Typical of *M. californica* is a groove on the dorsal side of the shaft that does not extend distad beyond the midlength of the bone (character 1) and a relatively short tarsometatarsus with a spur positioned farther away from its distal end (character 2). Males of *M. gallopavo* are best distinguished by their size (character 2), whereas those of *M. ocellata* are characterized by a spur positioned closer to the distal end of the bone (character 2) and by a greater rotation of Trochlea metatarsi II (character 3).

CHARACTER 1. Shaft, dorsal view [redefined from Steadman (1980)].

State A (*M. ocellata*: 94%, N = 16; and *M. gallopavo*: 83%, N = 46): The anterior groove on the Facies dorsalis of the shaft is deep and long (it extends distad beyond the midlength of the bone).

State B (*M. californica*: 67%, N = 205): The anterior groove on the Facies dorsalis of the shaft is usually shallower (sometimes it can be deep, but only in the proximal part), and it is short (i.e., it does not extend distad beyond the midlength of the bone).

CHARACTER 2. Combination of (a) absolute value of measurement A (total length) and (b) position of the spur, expressed as a ratio of measurement A and I (distance between spur core and Trochlea metatarsi III).

State A (*M. gallopavo*: 100%, N = 21): Total length of bone (measurement A) is 156 mm or larger.

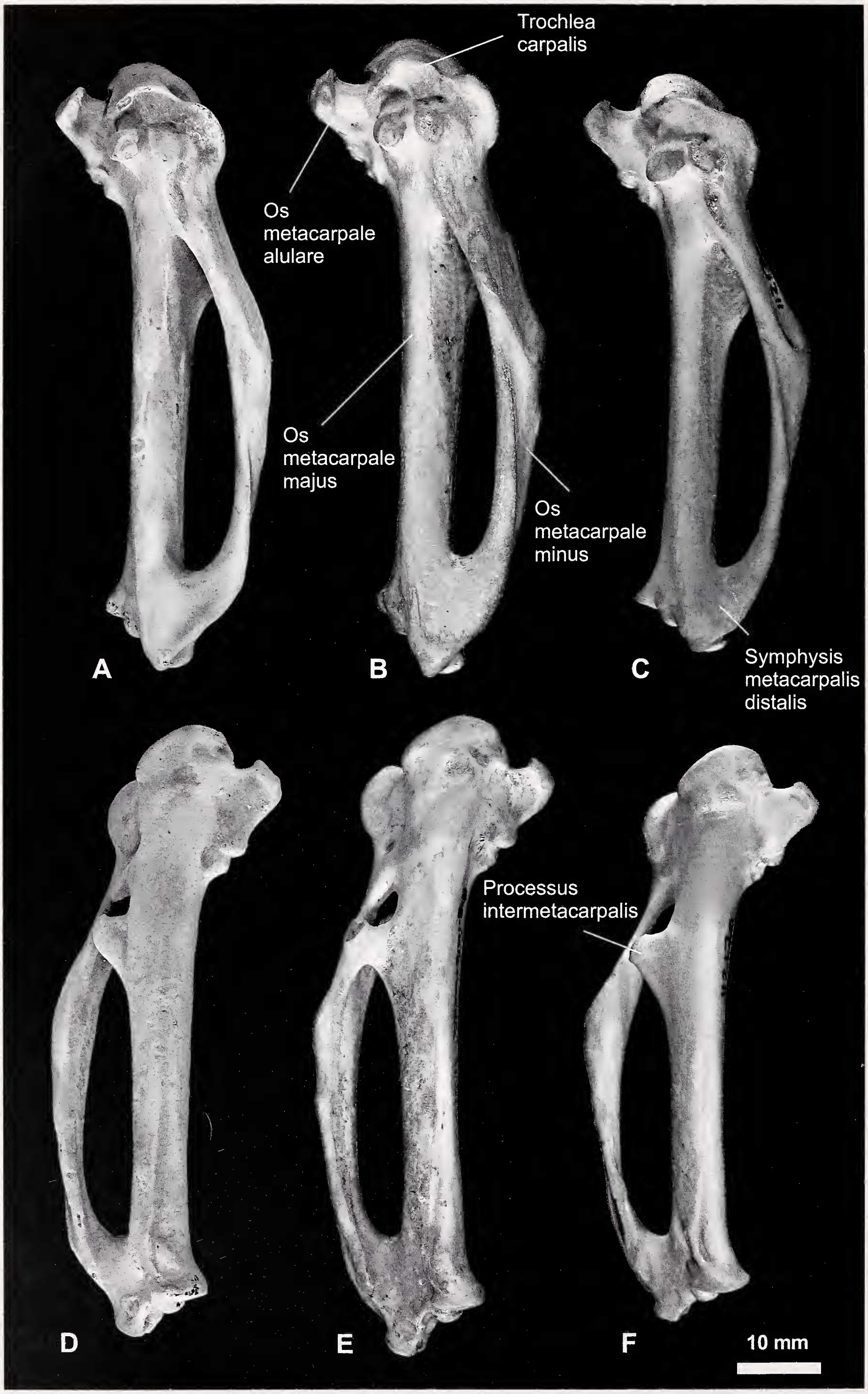
State B (*M. californica*: 91%, N = 135): Total length of bone (measurement A) is 151 mm or smaller, and the spur is situated somewhat farther from the distal end of the bone (ratio of measurements A:I is ≤ 2.25).

State C (*M. ocellata*: 100%, N = 9): Total length of bone (measurement A) is 151 mm or smaller, and the spur is situated somewhat closer to the distal end of the bone (ratio of measurements A:I is ≥ 2.28).

NB: See Table A14 for measurements and Figure 26 for scatter diagram of measurements A and I. This character is applicable only to complete tarsometatarsi of adult males. Special caution is necessary to differentiate between *M. californica* and *M. ocellata* because so few

←

Figure 18 Right radius in anterior (G–I, with enlargements D–F and M–O) and posteroventral (J–L, with enlargements A–C and P–S) views. *Meleagris californica* (A, D, G, J, M, and P; LACMHC D9790); *M. gallopavo* (B, E, H, K, N, and R; LACM 112154); *M. ocellata* (C, F, I, L, O, and S; LACM 112170). In *M. ocellata*, the proximal end is rotated more anteroventrad, which results in (a) Facies articularis ulnaris being at an angle to the long axis of the bone and (b) a clear slanting of the Cotyla humeralis (character 1; views I, F *vs.* G, D and H, E), whereas the distal end is rotated more posteriad, which results in (a) a steep transition between the shaft and the midpart of Facies articularis radiocarpalis and (b) a larger and more visible ridge at the anterior end of the Facies articularis radiocarpalis (character 2; views L, S *vs.* J, P and K, R). In *M. californica*, the dorsal edge of Facies articularis radiocarpalis curves into the anterior side of the radius (character 3; views G, M *vs.* H, N and I, O).


Trochlea carpalis
Os metacarpale alulare
Os metacarpale majus
Os metacarpale minus
A
B
C
Symphysis metacarpalis distalis
Processus intermetacarpalis
D
E
F
10 mm

specimens of *M. ocellata* were available, and measurements of this element of the two species overlap.

CHARACTER 3. Rotation of Trochlea metatarsi II, expressed as ratio of measurements F and G.

State A (*M. ocellata*: 69%, N = 16): Trochlea metatarsi II is rotated more in a plantar direction, which results in relatively greater values of measurement G; the ratio of measurements F:G is ≤ 1.65.

State B (*M. gallopavo*: 91%, N = 45; *M. californica*: 97%, N = 467): Trochlea metatarsi II is rotated less in a plantar direction, which results in relatively smaller values of measurement G; the ratio of measurements F:G is ≥ 1.7.

NB: See Table A14 for measurements and Figure 27 for scatter diagram of measurements F and G.

PES PHALANX 1, DIGIT 3

There is only one character on this bone, but it is very good for differentiating *M. ocellata* from the other two species of turkeys (Fig. 28).

CHARACTER 1. Lateral view.

State A (*M. ocellata*: 82%, N = 17): Dorsal margin of the bone clearly curves in a plantar direction near the distal end, so the Trochlea articularis is below an imaginary line going through the proximal part and midshaft.

State B (*M. gallopavo*: 100%, N = 44; and *M. californica*: 99%, N = 344): Dorsal margin of the bone is approximately straight, such that the dorsal margin of Trochlea articularis is at the same level as the proximal part and seldom at the same level as the midshaft, which is slightly lower.

NB: This character can be checked easily by putting the phalanx on a flat surface, with the dorsal side down. No difference was observed between juvenile and adult specimens in fossil and modern species.

DISCUSSION, COMPARISONS, AND COMMENTS

SEXUAL SIZE DIMORPHISM

Although sexual size dimorphism is very pronounced in turkeys, there are few osteological studies that provide reliable information on the extent of this type of dimorphism. In the most complete study, Steadman (1980) lists measurements of long bones separately for males and females of extant as well as fossil species. In his paper, extant *M. gallopavo* was well represented (up to 45♂, 34♀), but his measurements were biased toward *M. g. silvestris* (up to 33♂, 20♀) and *M. g. osceola* (up to 10♂, 11♀), which greatly outnumbered individuals of other subspecies. This bias toward any one subspecies is not present in our study, although the total number of specimens in our study did not match that of Steadman's (1980). In that our set of measurements differs to some extent from that of Steadman (1980), the two studies are complementary. Our results indicate that, regardless of the subspecies, the size ranges of males and females partly overlap only in measurements whose absolute values are relatively small, such as widths or depths of bones (Tables A1–A15). The measurements for "total length" of any long bone do not overlap between the sexes: that is, the smallest males are always larger than the largest females. This means that the size differences between sexes are larger than those between subspecies. Our observations on the lack of an overlap zone between the sexes of *M. gallopavo* agree with Steadman's (1980) data for "total length" measurements.

Unfortunately, we had too few sexed specimens of *M. ocellata* to analyze sexual size dimorphism in that species. However, Steadman's (1980) data show that, as with *M. gallopavo*, the sexes of *M. ocellata* do not overlap in measurements for "total length" of any long bone.

Sexual size dimorphism in *M. californica* was reported in previous studies. Howard (1927) listed measurements of the humerus and tarsometatarsus separately for males and females, and Steadman (1980) did the same for all major bones. We decided to extend the analyses to a much larger sample of specimens and to go into more details of sexual size dimorphism in this extinct species. We observed what we interpret to be similarly pronounced sexual size dimorphism in *M. californica*, where "total length" measurements of all elements with an adequate sample number of specimens did not overlap between the sexes (Tables A4–A15). In these cases the specimens were sexed by plotting for every element its length and another measurement on a graph. The scatter plots gave a distinct bimodal picture in all

←

Figure 19 Right carpometacarpus in ventral (A–C) and dorsal (D–F) views. *Meleagris californica* (A, D; LACMHC E6666); *M. gallopavo* (B, E; LACM 112167); *M. ocellata* (C, F; LACM 89958). In *M. ocellata* (C), the notch in the ventral rim of Trochlea carpalis is very shallow and broad as opposed to that in *M. gallopavo* (B), with *M. californica* being of either state (A represents the shallow form). The relative width of the proximal part and the midwidth of the carpometacarpus differ between *M. gallopavo* and *M. californica*, with *M. ocellata* being intermediate (B *vs.* A), but this character can best be checked by comparing measurement C and the ratio of measurements C and F (for details see character 2 and Fig. 20).

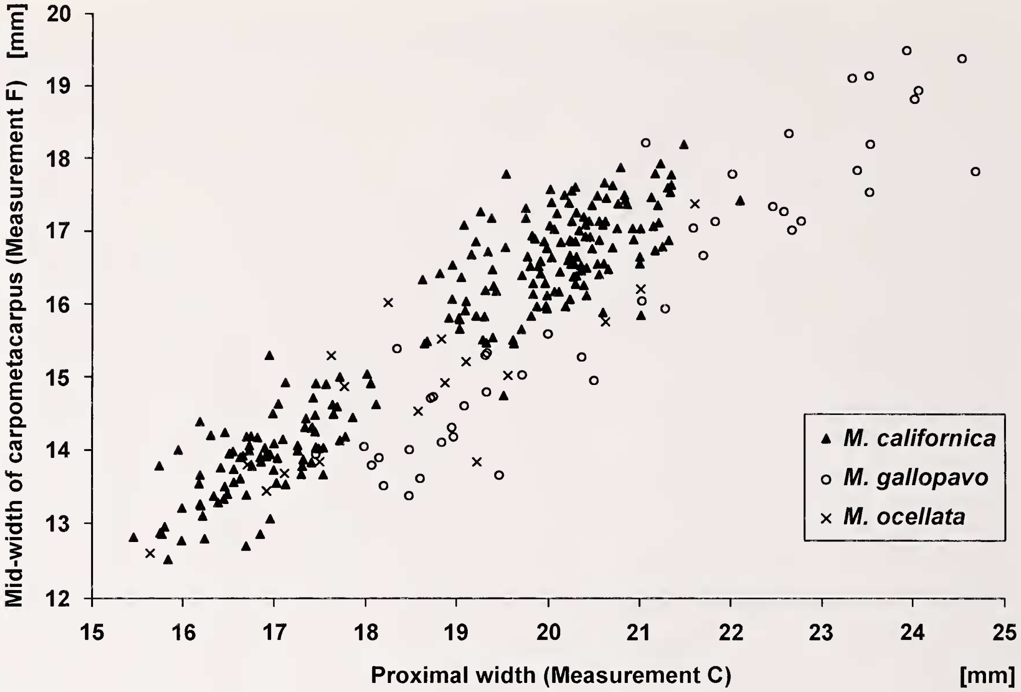


Figure 20 Carpometacarpus: Scatter diagram of measurements C and F (refers to carpometacarpus character 2, Table A10, and Fig. A5). In *M. californica*, the midwidth of carpometacarpus (measurement F) is relatively larger than that in *M. gallopavo*, with *M. ocellata* being intermediate. In addition, the absolute value of the proximal width (measurement C) is useful in telling apart larger specimens of *M. gallopavo* and smaller specimens of *M. californica*.

elements analyzed; a few examples are shown in Figs. 29–32. In seven cases (coracoid, scapula, humerus, ulna, radius, wing phalanx, and tibiotarsus), females were clearly separated from males without any intermediate specimens. In the remaining five cases (sternum, carpometacarpus, femur, tarsometatarsus, and pes phalanx), several specimens (one to eight, depending on the bone) were between the ranges typical of females and males, and consequently they were excluded. These few intermediate-sized specimens most probably represent subadult males. Having defined the sex of a specimen on the basis of one measurement (usually its length), we added its remaining measurements to the male or female database, whichever was appropriate. Further examples of bimodal distribution of measurements can be seen in scatter plots illustrating characters on the sternum, humerus, ulna, carpometacarpus, and tarsometatarsus (Figs. 11, 15, 17, 20, and 27). Although in all cases but one the measurements plotted there are different than the "total length," they practically do not overlap between the sexes.

We felt justified in defining the size ranges of males and females of *M. californica* because hundreds of specimens fell into one of two specified categories, and, as mentioned above, a similar situation is observed in both species of extant turkeys. Our data, based on very rich material and detailed analyses, are complementary to previous studies, especially that of Steadman (1980).

SEX RATIOS AND POSSIBLE SIZE DIFFERENCES OVER TIME

After sexing complete specimens in the way described above (i.e., by means of scatter plots, on the basis of their total length), we calculated the sex ratios for seven of the major, more numerous skeletal elements (tarsometatarsus, tibiotarsus, femur, coracoid, humerus, ulna, and carpometacarpus) of *M. californica*. Specimens represented only by proximal or distal ends were sexed in the same way, but on the basis of one measurement chosen on their preserved end (Table 1). For the partial specimens, the set limits (maximum measurements for females and minimum measurements for males) might sometimes differ slightly from what is given in Tables A5, A7, A8, A10, and A12–A14 because without knowing the best sexing factor (i.e., total length), we preferred to eliminate a few more intermediate specimens rather than sex them incorrectly. This procedure allowed us to include more specimens in the analyses than if we relied only on complete specimens. The carpometacarpus is the only element we decided to sex on the basis of just

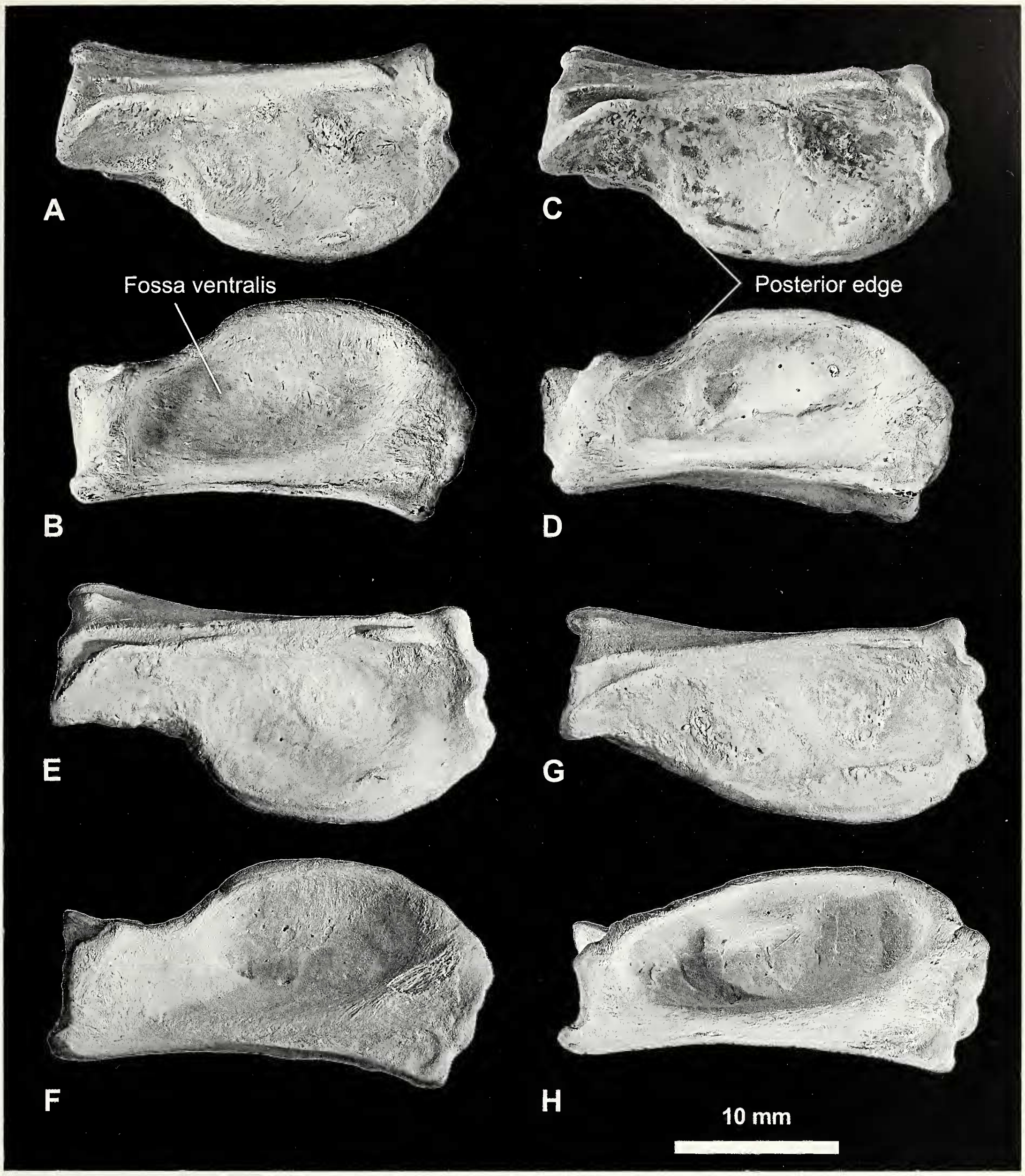


Figure 21 Right phalanx proximalis digiti majoris in dorsal (A, C, E, and G) and ventral (B, D, F, and H) views, proximal to left. *M. californica* (two specimens: A, B, LACMHC K8207; C, D, LACMHC K8209); *M. gallopavo* (E, F; LACM 112167); *M. ocellata* (G, H; LACM 112170). In *M. ocellata*, the proximal edge of the Fossa ventralis is steep and easily defined, and the proximal part of the posterior edge is approximately straight (both characters: H *vs.* B, D, and F).

one measurement (total length) because nearly all carpometacarpi were complete.

Interestingly, the sex ratios obtained from particular skeletal elements showed considerable differences (Table 2). Both sexes were equally represented by numbers of tarsometatarsi and tibiotarsi. The sex ratios seemed to be biased in favor of males for the femur and coracoid (male:female ratio was about 1:1.3), although the differences were statistically insignificant. However, sex ratios calculated from the wing elements (humerus, ulna, and carpometacarpus) were strongly skewed in favor of males, with all cases being statistically significant (chi-square test for testing equality of sex ratio). Since avian taphonomy is a very complex science, to address

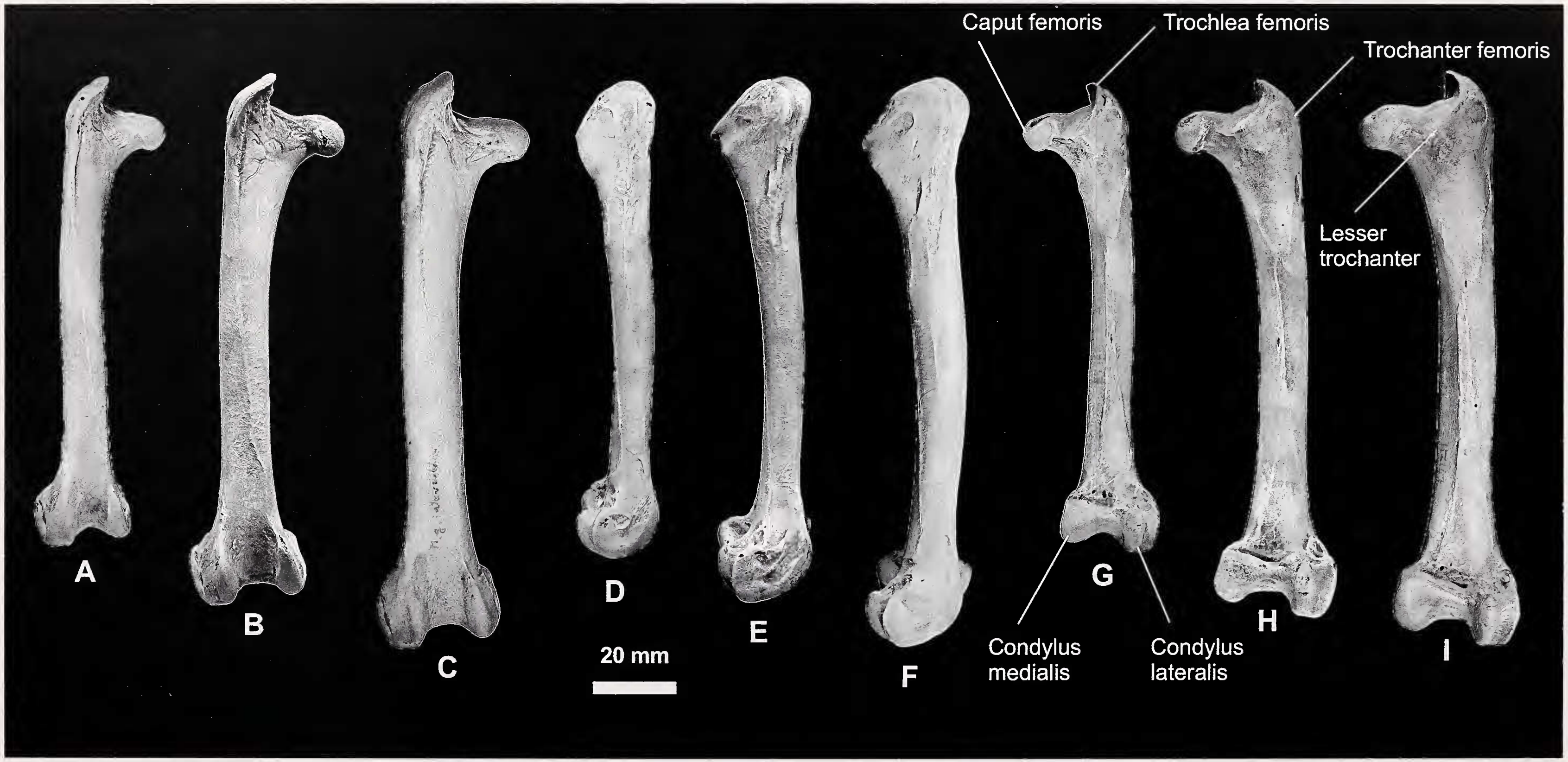


Figure 22 Right femur in anterior (A–C), lateral (D–F), and posterior (G–I) views. *Meleagris californica* (B, E, and H; LACMHC K7454); *M. gallopavo* (C, F, and I; LACM 112167); *M. ocellata* (A, D, and G; LACM 89958). In *M. ocellata*, the Lesser trochanter is not grooved, or it has only a very shallow transverse depression, as opposed to the other two species (character 1; views D, G *vs*. E, H and F, I).

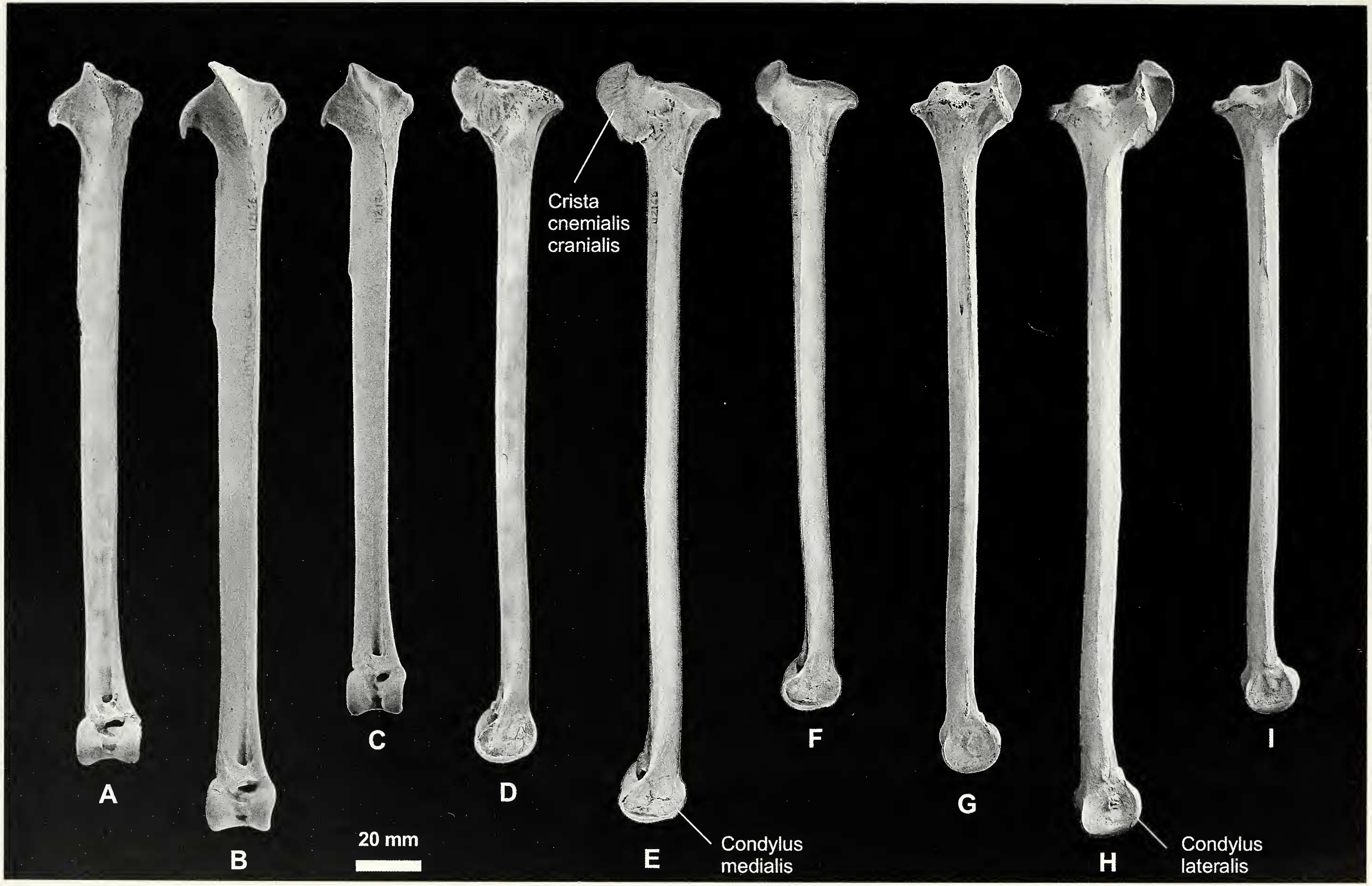


Figure 23 Right tibiotarsus in anterior (A–C), medial (D–F), and lateral (G–I) views. *Meleagris californica* (A, D, and G; LACMHC K7455); *M. gallopavo* (B, E, and H; LACM 112166); *M. ocellata* (C, F, and I; 112170). Typical of *M. ocellata* is a bent, or curving, Crista cnemialis cranialis (character 2; view C *vs.* A and B), whereas structures typical of *M. californica* include a narrow Crista cnemialis cranialis (character 1; view D *vs.* E and F) and a small, slightly protruding knob on the distal end (character 3; view G *vs.* H and I).

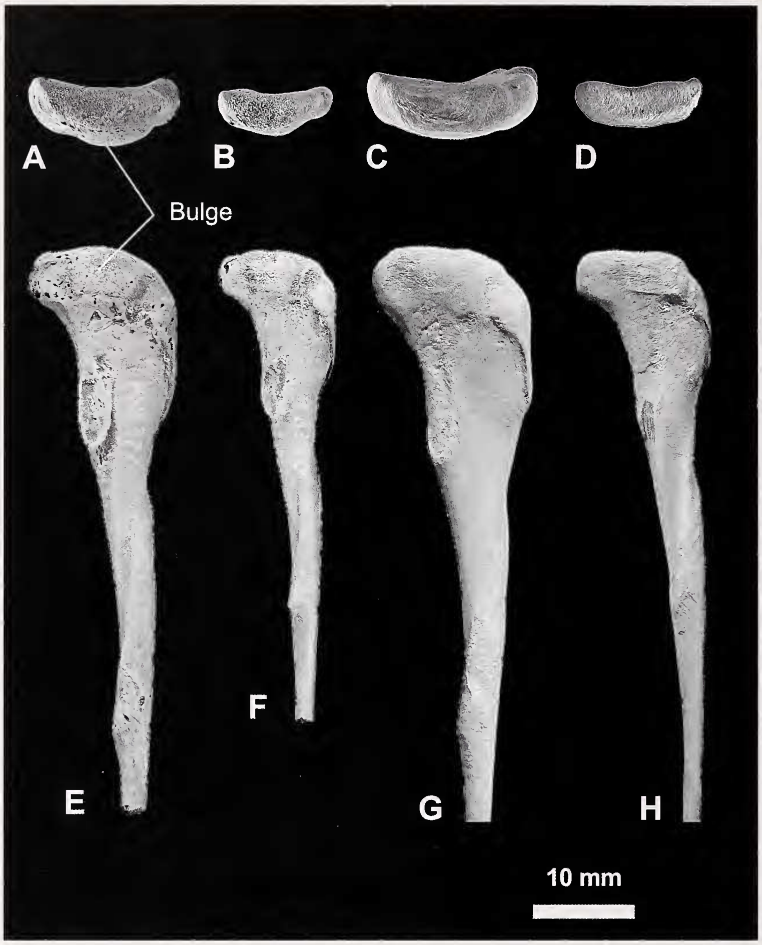


Figure 24 Right fibula in proximal and lateral views. *Meleagris californica* (two specimens: A, E; LACMHC K8377; B, F; LACMHC K8380); *M. gallopavo* (C, G; LACM 112167); *M. ocellata* (D, H; LACM 112170). *Meleagris californica* differs from the other two taxa by having a relatively larger bulge on the middle part of the proximal end.

this matter properly, it is necessary to analyze in detail the fragmentation and preservation of turkey bones and compare the results with those of other species found at Rancho La Brea. Proper analyses of this type would take too much space here. Therefore, we will treat this in greater depth elsewhere. At this stage, it seems reasonable to assume tentatively that because turkeys and other victims of the asphalt seeps were first trapped by their legs, with the rest of their body exposed to predators, scavengers, and weathering, the lower leg elements (tarsometatarsus and tibiotarsus) are more likely to reflect the actual sex ratio more closely than the elements positioned farther away from the ground level. The degree of damage to the bones of avian prey depends not only on the involved species but also on the relative size of the predator/victim (e.g., Bocheński, 2005). It is possible that because of the large sexual size dimorphism in turkeys, particular body parts of one sex suffered somewhat different damage than those of the other sex. It is also possible that some other sex-related factors, such as behavior or weight, played a role here and resulted in the upper body parts of one sex remaining more often on the surface of the asphalt seep, where they were exposed to weathering, instead of being buried in the asphalt. Thus, we tentatively postulate that, based on the lower leg elements, the sex ratio of *Meleagris californica* was close to 1:1. A similar sex ratio (i.e., close to 1:1) is observed in the poults of modern *M. gallopavo* at the time of hatching, and the ratio of adult males to adult females of this species varies widely with the area and the year, with gobblers prevailing in populations that are not hunted (Schorger, 1966).

We checked for possible differences in size between populations of different geological ages by comparing measurements of sexed specimens coming from "old" and "young" pits by means of factorial two-way (sex and age) ANOVA. We ran a number of tests for several skeletal elements applying the following: (a) age criteria developed by Howard (1962b) on the basis of bird census

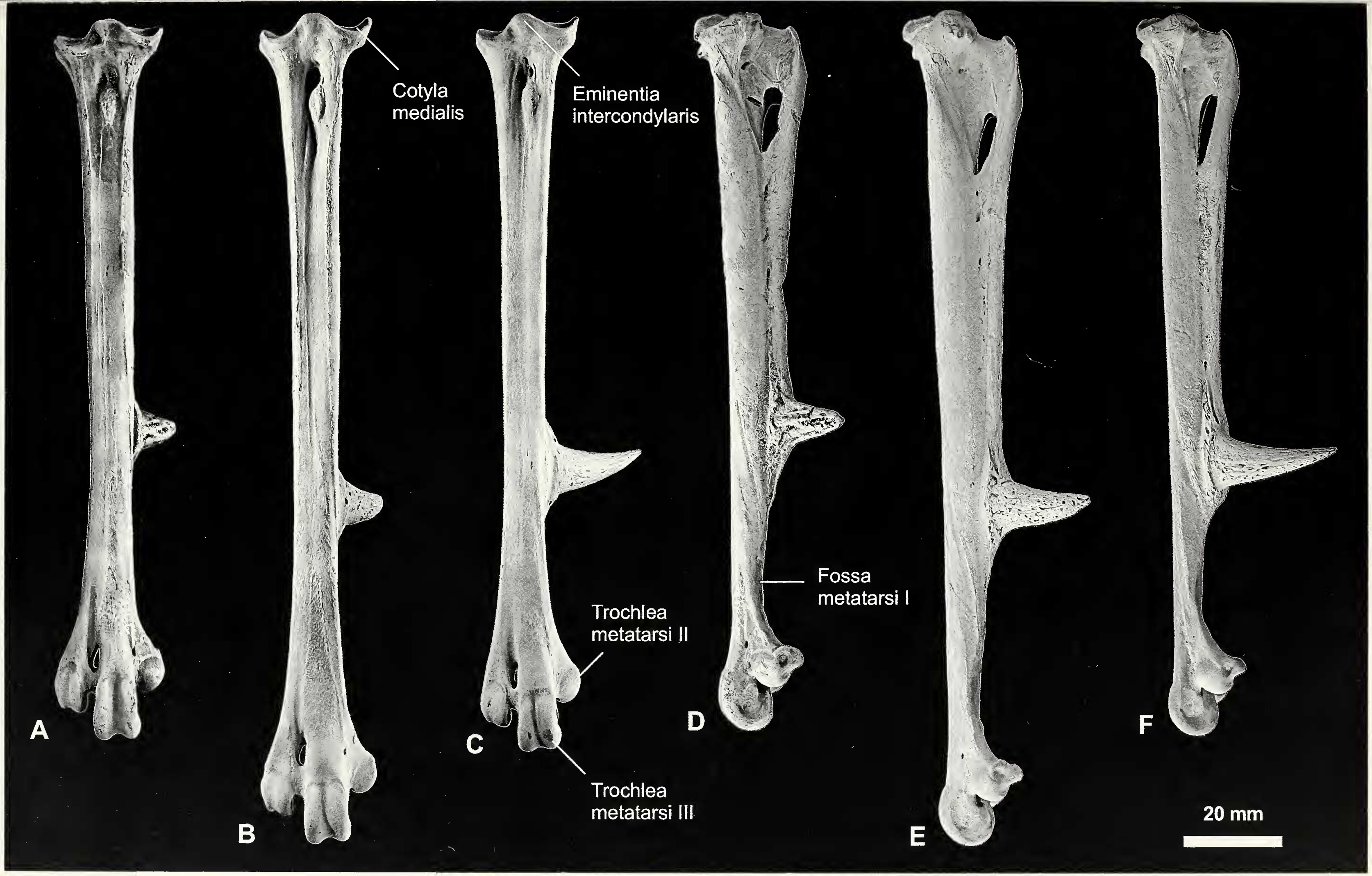


Figure 25 Right tarsometatarsus in dorsal (A–C) and medial (D–F) views. *Meleagris californica* (A, D; LACMHC E6173); *M. gallopavo* (B, E; LACM 112431); *M. ocellata* (C, F; LACM 112170). In *M. californica*, a groove on the dorsal side of the shaft is usually shallow, and it does not extend distad beyond the midlength of the bone (character 1; view A *vs.* B and C). In *M. ocellata*, Trochlea metatarsi II is rotated more in a plantar direction, but this character can best be checked by comparing the ratio of measurements F and G (see character 3 and Fig. 27). Moreover, males of *M. gallopavo* can be best distinguished by their large size (measurement A), whereas in males of *M. ocellata* the spur is situated somewhat closer to the distal end of the bone than it is in males of *M. californica*, but this character can best be checked by comparing measurement A and the ratio of measurements A and I (for details see character 2 and Fig. 26). More comments on the eye-catching differences in the length of the spur are in "Discussion, Comparisons, and Comments."

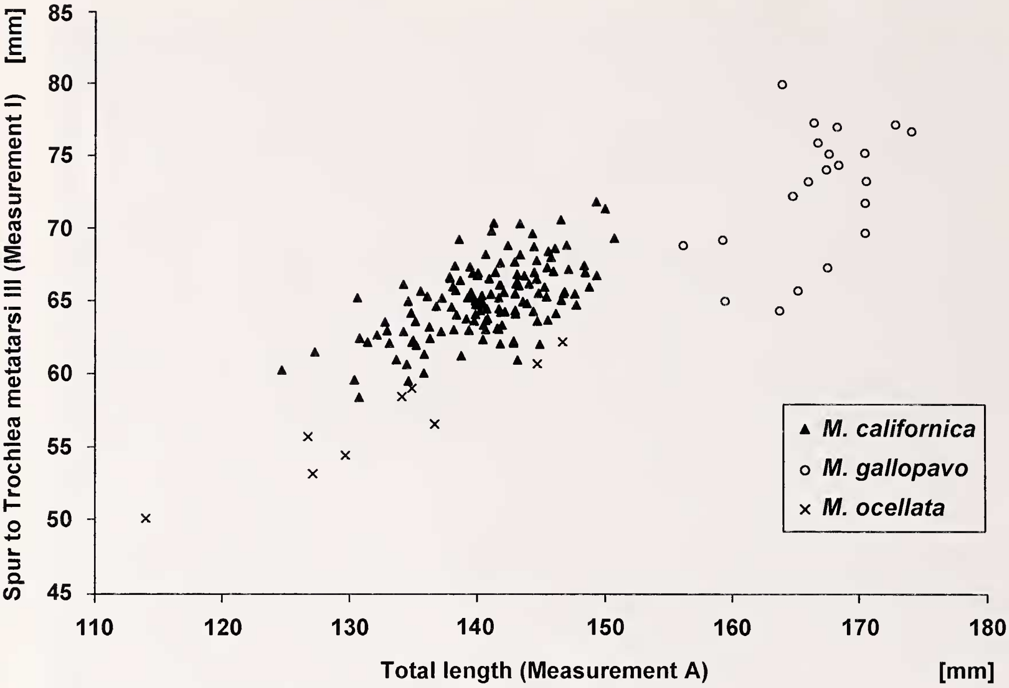


Figure 26 Tarsometatarsus: Scatter diagram of measurements A and I (refers to tarsometatarsus character 2, Table A14, and Fig. A6). Males of *M. gallopavo* can best be distinguished by their large size (measurement A), which does not overlap with those of the other two species. Males of *M. ocellata* tend to have their spur positioned closer to the distal end of the bone (measurement I relatively smaller in bone of the same length) than it is in *M. californica.*

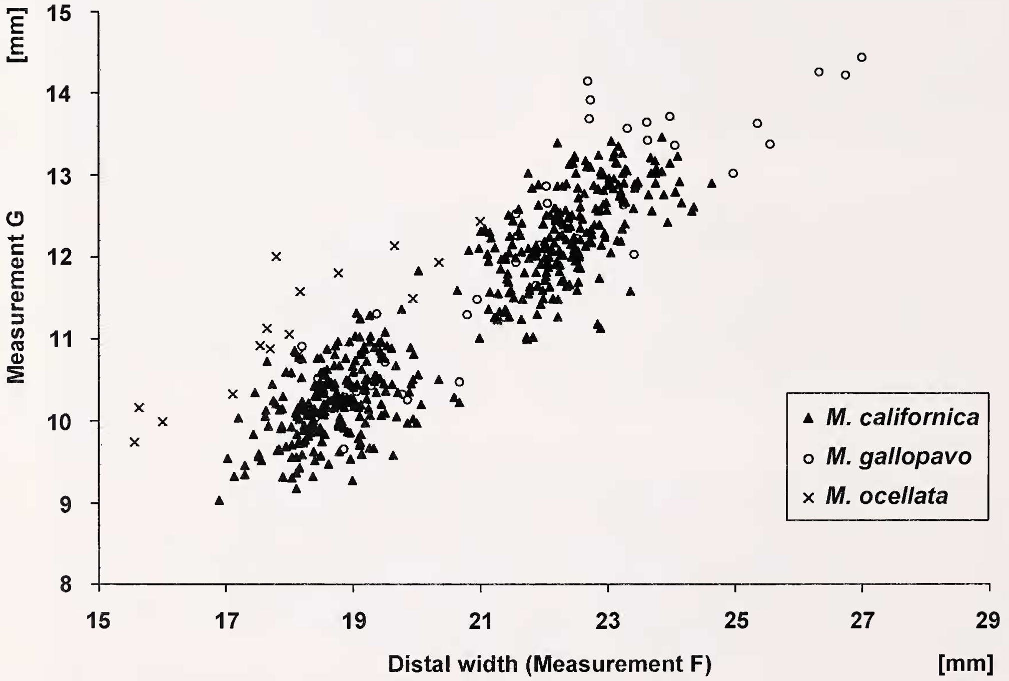


Figure 27 Tarsometatarsus: Scatter diagram of measurements F and G (refers to tarsometatarsus character 3, Table A14, and Fig. A6). Most specimens of *M. ocellata* can be distinguished from the other two taxa by a greater plantar rotation of Trochlea metatarsi II, which is reflected in the relatively greater values of measurement G. The other two species, *M. californica* and *M. gallopavo*, cannot be told apart by this criterion.

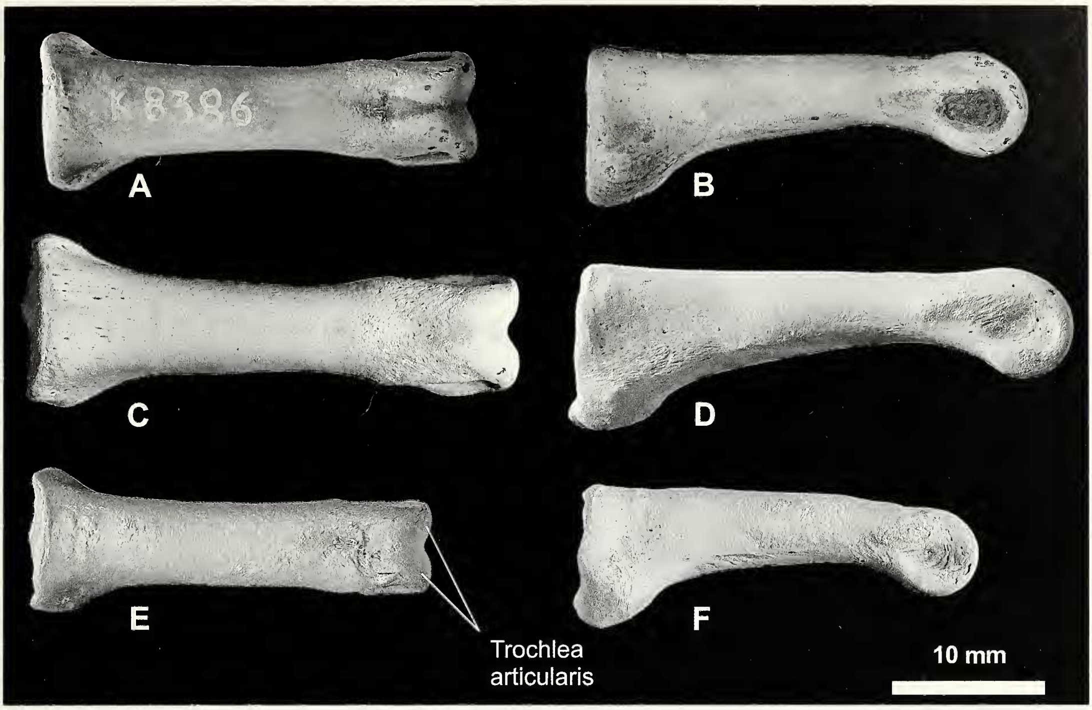


Figure 28 Right Pes phalanx 1, digit 3 in dorsal (A, C, E) and lateral (B, D, F) views. *Meleagris californica* (A, B; LACMHC K8386); *M. gallopavo* (C, D; LACM 112165); *M. ocellata* (E, F; LACM 89958). In *M. ocellata*, the dorsal margin of the bone clearly curves in a plantar direction near the distal end.

(older pits: 3, 4, 13, 16, 61–67, and 77; younger pits: 28, 36, 37, A, and Academy); (b) age criteria recalculated by Marcus and Berger (1984) on Howard's (1962b) "critical" extinct species (older pits: 4, 13, 60, and 77; younger pits: 3, 16, and 61–67); and (c) Marcus and Berger's (1984) radiocarbon dates. Contrary to expectations, the latter criterion proved to be particularly difficult to apply because of extensive mixing of deposits within many pits, and for that reason we used here several combinations of "old" and "young" pits by selecting specimens according to not only their pit numbers but also their coordinates and depth of deposit. None of our attempts resulted in finding any unquestionable size differences between populations derived from "old" and "young" pits. We recognize that our negative results do not necessarily mean that turkeys from older deposits did not differ in size from their younger counterparts because a great majority of turkey remains come from only two pits (Pit 16 and Pit 4), which probably cover a similar age span and both of which are particularly difficult to interpret in terms of their stratigraphy and radiocarbon dates (Marcus and Berger, 1984). On the other hand, some of the above-mentioned categories of pits, especially the "younger" ones, included just a few or a dozen specimens. Moreover, large sexual and individual variation in size hampered the analyses.

We also failed to find any consistent differences in morphology between specimens from excavation pits attributed to different geological ages. Again, this can result from the lack of such differences, the low number of specimens from pits other than Pit 16 and Pit 4, and/or significant individual variation in most characters.

NOTES ON THE QUALITATIVE CHARACTERS DESCRIBED

Of the 55 characters described (Table 3), 51 show two states (A and B). In two-state characters, one state is typical of one species only and therefore distinguishes that species from the other two. Three of the 51 characters (sternum, character 8; carpometacarpus, characters 1 and 2) serve to distinguish two species only, with the third species tending to overlap the condition in the other two. Most characters are unique to *Meleagris ocellata* (25). The number is somewhat lower for *M. californica* (18), and only five characters are unique to *M. gallopavo*. Four other characters show three states (A, B, and C), each of which is species specific (furcula, character 3; sternum, character 5; ulna, character 1; tarsometatarsus, character 2). Metrical differences between *M. gallopavo* and *M. ocellata* are discussed in greater detail in Bocheński and Campbell (2005).

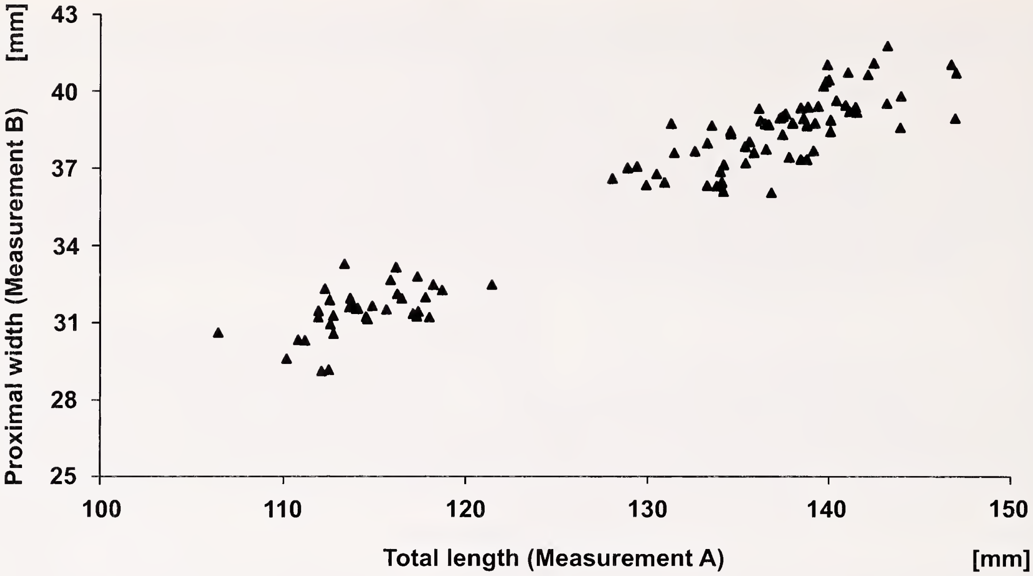


Figure 29 Humerus of *M. californica*: Scatter diagram of measurements A and B (see Table A7 and Fig. A3) used to sex the specimens. The diagram includes all of the 101 specimens that had both measurements taken. All specimens fall into one of the two distinct groups, which are interpreted as females (36 specimens) and males (65 specimens). Although there is a zone of no overlap in each of the measurements, measurement A (total length) was chosen as the main criterion to sex the specimens because there were 10 extra, partly damaged specimens (seven thought to be females and three males), with measurement A taken and measurement B missing. Based on the diagram, the maximum value of measurement A for the females is 121.44 mm, and the minimum value of measurement A for the males is 128.06 mm.

The number of characters described for particular elements varies considerably. No characters were found on the pelvis, which might result from its poor state of preservation in fossil specimens of *M. californica*. Only one character was described for the scapula, femur, fibula, and Pes phalanx 1, digit 3. The most characters were found for the sternum and coracoid, each of which yielded eight characters.

In terms of the number and quality of characters, the most diagnostic regions of the skeleton are the head (premaxilla, mandible, skull, and quadratum), sternum, and parts of the shoulder girdle (furcula, coracoid). More than half of all distinguishing characters were described on those elements.

All but one of the characters described are imperfect because they are found in a certain number of "atypical" individuals in one or more species. Although few authors directly admit it, this seems to be a general phenomenon observed within various groups of closely related birds whenever the number of specimens examined is relatively large. For instance, such variations were observed in grebes (Bocheński, 1994), corvids (Tomek and Bocheński, 2000), and turkeys (Steadman, 1980). Most probably these variations result from a mixture of genetic and environmental factors, and such variability indicates that few small morphological differences can be assumed to have significance for distinguishing species. Also, Schorger (1966, and references therein) stresses that turkey species are very plastic. Obviously, many small, but nevertheless valid, osteological characters differentiating closely related species are not crucial for the survival of particular individuals. They are "typical" for the species in the sense that they occur in a clear majority of individuals, but their potential significance for the species can be very hard to determine in regular functional-morphological analyses because such small differences reflected on skeletal elements are difficult to interpret.

FOSSIL TURKEYS FROM LOCALITIES OTHER THAN RANCHO LA BREA

Fossil turkey remains from all other localities housed in the Vertebrate Paleontology Section of the Natural History Museum of Los Angeles County were checked for the qualitative characters found on the three main species investigated. The localities are in California, New Mexico, Washington, and Mexico. This survey allowed us to verify the species identification and the known range of *M. californica* and *M. crassipes*.

LATE PLIOCENE (BLANCAN)

University Drive, Orange County, California (Locality LACM 3978). Femur, distal, right,

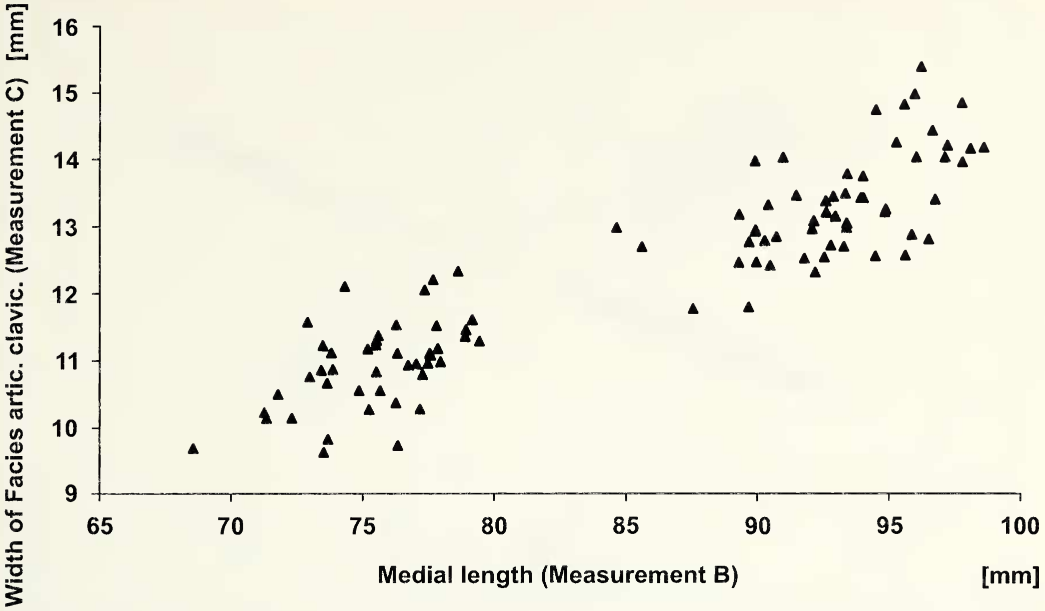


Figure 30 Coracoid of *M. californica*: Scatter diagram of measurements B and C (see Table A5 and Fig. A2) used to sex the specimens. The diagram includes all of the 99 specimens that had both measurements taken. All specimens fall into one of the two distinct groups, which are interpreted as females (44 specimens) and males (55 specimens). Of the two measurements, the medial length (measurement B) was chosen as the main criterion to sex the specimens because the ranges of the two groups do not overlap. Subsequently, 10 extra, partly damaged specimens (four thought to be females and six males), with measurement B taken and measurement C missing, were included in the sex-specific database. Based on the diagram, the maximum value of measurement B for the females is 79.44 mm, and the minimum value of measurement B for the males is 84.61 mm.

LACM 64001. Only one specimen of a turkey is known from this locality. Steadman (1980) identified it as *Meleagris* sp. and noted that "it documents the earliest known occurrence of a turkey in southern California." We were unable to provide a species identification because we did not find any reliable characters on the distal femur.

Taunton Substation, Adams County, Washington (Locality LACM 6408). Tarsometatarsus, proximal, left, LACM 10715; tarsal spur, left, LACM 150992. These specimens are catalogued as Meleagrididae. It is unfortunate that they are too damaged to be identified more precisely because they are the only record of turkeys from the Pacific Northwest.

EARLY PLEISTOCENE (IRVINGTONIAN)

Vallecito Creek, San Diego County, California (Locality LACM 1358). Several specimens (Howard, 1963). Turkey remains from this locality were described as a new species, *Meleagris anza* (Howard, 1963). The two humeri, which bear the same catalogue number, LACM 3753, were described as the holotype and paratype. These humeri show State B of our character 1 (i.e., as in *M. californica*) and State A of our character 3 (i.e., as in *M. ocellata*). This appears to be a unique combination of character states, but more specimens are needed to check for possible individual variation. The striking flatness of the bones discussed by Howard (1963) and Steadman (1980) is probably a natural condition rather than the result of crushing because it is present in both humeri, and critical areas of the bone show no displacement along cracks. The other elements ascribed to that species also show a unique combination of characters. Additional specimens from this area appear to represent at least two species. A more detailed analysis of these species will appear separately.

LATE PLEISTOCENE (RANCHOLABREAN)

Carpinteria, Santa Barbara County, California (Locality LACM 139). The fossil material consists of a few to several dozen specimens of each major element, including the skull and sternum. The specimens lack individual catalogue numbers and are group catalogued as *Parapavo californicus*. In most cases, the states of the characters we identified (see above) agree with those typical of *M, californica* (with a few "atypical" specimens allowed, as in the material from Rancho La Brea). Therefore, we agree with the identification of this material as *M. californica* by L. Miller (1927, 1942), Wetmore (1931), Brodkorb (1964a), and Steadman (1980).

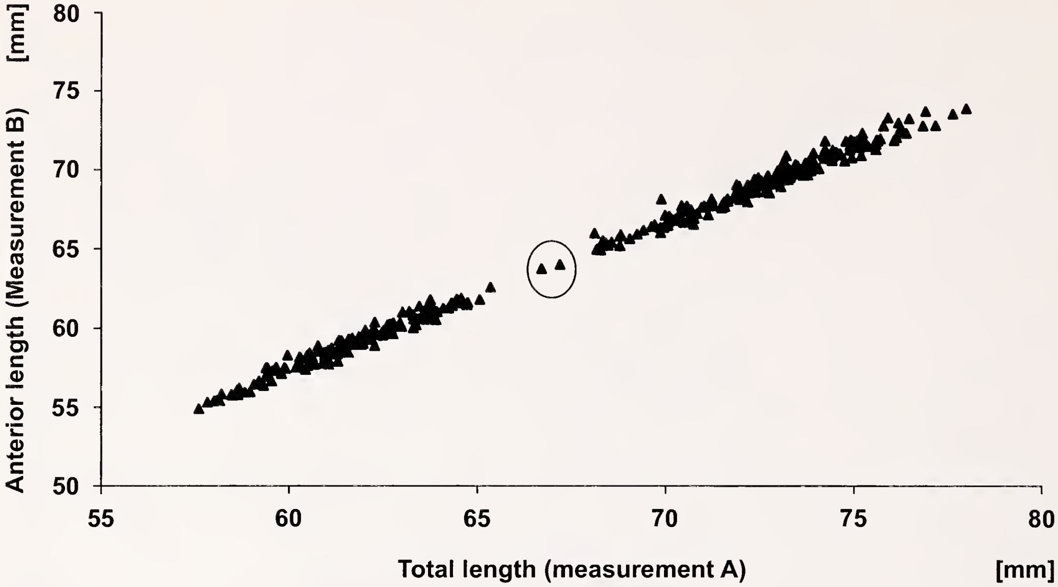


Figure 31 Carpometacarpus of *M. californica*: Scatter diagram of measurements A and B (Table A10 and Fig. A5) used to sex the specimens. The diagram includes all of the 346 specimens that had both measurements taken. With the exception of the two encircled specimens, all of the specimens fall into one of the two distinct groups, which are interpreted as females (137 specimens) and males (207 specimens). Of the two measurements, the total length (measurement A) was chosen as the main criterion to sex the specimens because its zone of no overlap was larger. Subsequently, five extra, partly damaged specimens (thought to be males), with measurement A taken and measurement B missing, were included in the sex-specific database. Based on the diagram, the maximum value of measurement A for the females is 65.35 mm, and the minimum value of measurement A for the males is 68.11 mm. The two encircled specimens were excluded because they most probably represent subadult males.

Workman and Alhambra Streets, Los Angeles County, California (Locality LACM 1023). Tibiotarsus, distal, right, LACM 982; and Pes phalanx 1, digit 4, left, LACM 981. Steadman (1980) identified the tibiotarsus as cf. *Meleagris*, whereas L. Miller (1942) and Brodkorb (1964a) considered it to be *P. californicus*, and W. Miller (1971) referred to it as cf. *Parapavo*. We find State B of our character 3 present, which is a condition typical of *M. californica*. The second specimen is certainly a turkey of the genus *Meleagris*, but further identification was not possible because we did not include this phalanx in our study. Our determinations agree with those of Howard (1936), who found that the two turkey specimens from the site do not have any diagnostic characters, but that they can probably be assigned to *Parapavo*.

Zuma Creek, Los Angeles County, California (Locality LACM 1754). Tibiotarsus, proximal, right; and cervical vertebra; both specimens have the same catalogue number, LACM 15833, and they are catalogued as *P. californicus*. The fragment of the tibiotarsus is badly damaged, and we did not include vertebrae in our study. Judging by their general appearance, both fragments can be assigned to *Meleagris* sp., but a more precise identification is not possible.

Highland Park District, Los Angeles County, California (Locality LACM/(CIT) 342). Coracoid, sternal end, right, CIT 3225. This specimen was identified by L. Miller (1942) as *P. californicus*. We find State B of our characters 1 and 8 of the coracoid present, which is typical of two species (i.e., *M. gallopavo* and *M. californica*, as opposed to *M. ocellata*). Therefore, we think that the original identification is somewhat too definitive, and we consider the specimen to be *Meleagris* sp.

Emery Borrow Pit, Orange County, California (Locality LACM 7053). Tarsometatarsus, trochlea of digit 2, right, LACM 100325. This specimen is catalogued as cf. *Meleagris*. We do not have any diagnostic characters on that part of the bone, and we are unable to identify it more precisely.

Imperial Highway, Orange County, California (Locality LACM 1052). Radius, distal, LACM 2009. This specimen shows State B of our character 3 and probably State B of our character 2, although it is partly damaged. These conditions are typical of *M. californica*. These characters are relatively reliable, and therefore we consider the identification to be well based. This contradicts Steadman (1980), who did not find good characters on this element and considered the specimen to be *Meleagris* sp., but it agrees with the original identification made by Howard (1936)

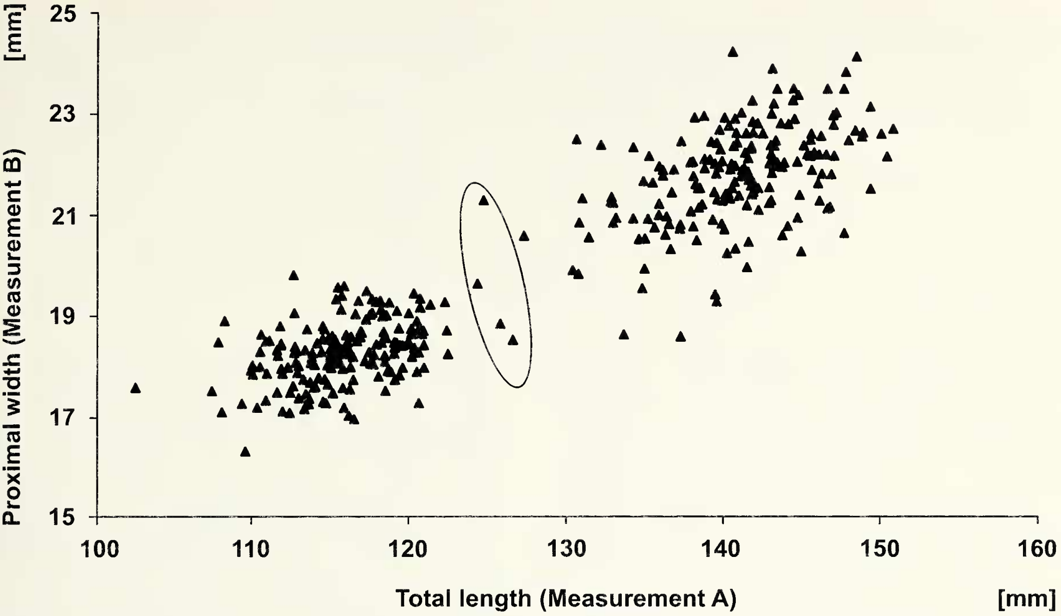


Figure 32 Tarsometatarsus of *M. californica*: Scatter diagram of measurements A and B (see Table A14 and Fig. A6) used to sex the specimens. The diagram includes all of the 353 specimens that had both measurements taken. With the exception of the four encircled specimens, all of the specimens fall into one of the two distinct groups, which are interpreted as females (170 specimens) and males (179 specimens). The total length (measurement A) was chosen as the main criterion to sex the specimens. Subsequently, 41 extra, partly damaged specimens (24 believed to be females and 17 males), with measurement A taken and measurement B missing, were included in the sex-specific database. Based on the diagram, the maximum value of measurement A for the females is 122.48 mm, and the minimum value of measurement A for the males is 127.29 mm. The four encircled specimens were excluded because they most probably represent subadult males.

and later confirmed by L. Miller (1942), Brodkorb (1964a), and W. Miller (1971).

La Mirada/Coyote Creek, Orange County, California (Locality 6689). Radius, complete, left, LACM 151473; Coracoid fragment, right, LACM 151474. W. Miller (1971) referred to these specimens as *P. californicus*. Steadman (1980) incorrectly referred to this radius as LACM 2009, when it was actually uncatalogued. Based on State B of our character 3 and size, we identify this specimen as *M. californica*.

San Josecito Cave, Nuevo León, Mexico (Locality LACM/(CIT) 192). Turkey remains from this site were described as *Meleagris crassipes* (L. Miller, 1940). Brodkorb (1964a, 1964b) placed the species in *Agriocharis*, but Steadman (1980) moved it back to *Meleagris*. We made no attempt to find characters exclusive for this species, although this would certainly be possible, at least on some elements. Instead, we confined ourselves to checking the remains for the characters found on the three main species investigated (Table 4). We found that *M. crassipes* shows a mosaic of conditions otherwise typical of different species, or pairs of species, of turkeys. This mosaic condition is especially

Table 1 Mensural criteria for sexing skeletal specimens of *M. californica*. Capital letters indicate appropriate measurements (mm) given in Tables A5, A7, A8, A10, and A12–A14 and illustrated in Figures A2–A7. Measurements before slashes are the maximum values for females, and those following the slashes are the minimum values for males.

	Measurements used to sex specimens		
Element	Complete element	Proximal end	Distal end
Coracoid	B: as in Table A5	D: 30.32/33.43	F: 21.18/22.86
Humerus	A: as in Table A7	B: 33.32/36.13	F: 25.50/27.97
Ulna	A: as in Table A8	C: 16.77/17.80	G: 15.32/16.29
Carpometacarpus	A: as in Table A10	—	—
Femur	B: as in Table A12	C: 26.19/28.89	G: 23.25/25.00
Tibiotarsus	A: as in Table A13	B: 20.05/22.60	E: 17.37/17.97
Tarsometatarsus	A: as in Table A14	B: 19.58/20.05	F: 20.07/21.07

Table 2 Sex ratio in *M. californica* calculated from seven major skeletal elements; data pooled for all the pits. Asterisks indicate statistically significant differences (* = $p < 0.05$; ** = $p < 0.01$).

Element	Number of males	Number of females	Male:female
Coracoid	61	46	1:1.33
Humerus	85	53	1:1.60**
Ulna	98	70	1:1.40*
Carpometacarpus	211	134	1:1.57**
Femur	70	52	1:1.35
Tibiotarsus	140	147	0.95:1
Tarsometatarsus	176	187	0.94:1

striking on the coracoid where seven characters were evaluated. Altogether, of the 14 characters evaluated on various elements, five were typical of *M. californica*, two of *M. ocellata*, one of *M. gallopavo*, four of *M. gallopavo* and *M. ocellata*, and two of *M. gallopavo* and *M. californica*. However, the numbers do not necessarily reflect the relative similarities between *M. crassipes* and the other species because they refer to only a few incidental characters checked only on those bones that were well preserved in the fossil collection, and therefore the set of characters is not completely representative.

Howell's Ridge Cave, Grant County, New Mexico (Locality LACM 1725). Original labels refer to this site as Hachita Cave. The four fossil turkey bones from this site were first described as *M. gallopavo* by Howard (1962a). Rea (1980) and Steadman (1980) listed the turkeys as *M. crassipes*. Of the four fossils, only three were preserved well enough to be checked. A coracoid (scapular end, right, LACM 33890) showed State B of our character 5 (i.e., as in *M. californica*) and State A of our character 7 (i.e., as in *M. gallopavo* and *M. ocellata*). A scapula (proximal, left, LACM 33889) showed State B of our character 1 (i.e., as in *M. gallopavo* and *M. californica*). An ulna (proximal, left, LACM 33892) showed State C of our character 1 (i.e., as in *M. californica*). The combination of characters on the coracoid and ulna is the same as that in *M. crassipes* from San Josecito Cave (the turkey scapula from that site is not known) (see Table 4). This unique combination of characters supports Rea's (1980) and Steadman's (1980) referral of the turkey fossils from Howell's Ridge Cave to *M. crassipes*.

Shelter Cave, Dona Ana County, New Mexico (Locality LACM 1010). Turkey fossils from this site were identified by Howard and Miller (1933) as *M. gallopavo* and by Rea (1980) as *M. crassipes*. A Pes phalanx 1, digit 3 (complete, right, LACM 657) showed State B of our character 1 (i.e., as in *M. gallopavo* and *M. californica*), whereas an associated Pes phalanx 2, digit 3 (also LACM 657) was not included in our study. The other remains (i.e., humerus, LACM 643; ulnae, LACM 556 and 557) were too fragmentary for identification. Rea (1980:212) based his identification on other criteria.

Conkling Cavern, Dona Ana County, New Mexico (Locality LACM 1009). The fossil turkeys from this site were identified as *Meleagris gallopavo* by Howard and Miller (1933) and Rea (1980). A humerus (shaft, right, LACM 21) showed State B of our character 2 (i.e., as in *M. gallopavo* and *M. californica*). A radius (distal, right, LACM 23) showed State B of our character 2 (i.e., as in *M. gallopavo* and *M. californica*) and State A of our character 3 (i.e., as in *M. gallopavo* and *M. ocellata*). A carpometacarpus (complete, right, LACM 22) showed State B of our character 1 (i.e., as in *M. gallopavo*). The remaining two fragments were either too damaged (sternum, caudal tip, LACM 144) or not included in our main study (pes phalanx, LACM 145) to check them for possible characters. The combination of characters on the humerus, radius, and carpometacarpus exclude *M. californica* and *M. ocellata* from consideration. The two characters on the humerus and carpometacarpus do not differentiate between *M. gallopavo* and *M. crassipes* (Table 4), but Rea (1980:212) eliminated the latter species based on other criteria. Therefore, it seems that these specimens can be assigned to *M. gallopavo*.

GEOGRAPHIC DISTRIBUTION

With one exception (Miller and Johnstone, 1937), which later turned out to be a different species (Miller and Bowman, 1956), the known records of *M. californica* have all been confined to California (Howard, 1927; Steadman, 1980). Because of damage to, and the scarcity of, turkey remains from most fossil sites, as well as large individual variation and an overall similarity in osteology between *M. californica* and *M. gallopavo*, the precise identification of fossil turkeys is often a difficult task. Based on our criteria, the unquestionable geographic range of *M. californica* extended from Orange County in the south (Imperial Highway), through Los Angeles County (Rancho La Brea and probable also Workman and Alhambra Streets), to Santa Barbara County in the north (Carpinteria). Unfortunately, fossil remains from the more northerly situated Potter Creek Cave in Shasta County, California (L. Miller, 1911, 1925), were unavailable during

Table 3 Cross reference of *Meleagris* species and characters typical of them. A question mark (?) indicates characters that turned out to be useless for distinguishing the species (too much individual variation and/or intermediate specimens).

Element	Character #	*M. californica*	*M. gallopavo*	*M. ocellata*
Premaxilla	1	B	A	A
	2	B	A	A
	3	B	A	A
	4	B	A	A
Mandible	1	B	A	B
	2	B	A	B
Quadratum	1	B	B	A
	2	B	B	A
Skull	1	B	B	A
	2	B	B	A
Furcula	1	B	B	A
	2	B	B	A
	3	C	A	B
	4	B	B	A
	5	B	A	A
	6	B	A	A
Sternum	1	B	A	A
	2	B	A	B
	3	B	A	B
	4	B	A	B
	5	C	B	A
	6	B	B	A
	7	B	B	A
	8	?	B	A
Coracoid	1	B	B	A
	2	B	A	A
	3	B	A	A
	4	B	A	A
	5	B	A	A
	6	B	B	A
	7	B	A	A
	8	B	B	A
Scapula	1	B	B	A
Humerus	1	B	A	A
	2	B	B	A
	3	B	B	A
	4	B	B	A
Ulna	1	C	A	B
	2	B	B	A
Radius	1	B	B	A
	2	B	B	A
	3	B	A	A
Carpometacarpus	1	?	B	A
	2	B	A	?
Phalanx proximalis digiti majoris	1	B	B	A
	2	B	B	A
Femur	1	B	B	A
Tibiotarsus	1	B	A	A
	2	B	B	A
	3	B	A	A
Fibula	1	B	A	A
Tarsometatarsus	1	B	A	A
	2	B	A	C
	3	B	B	A
Pes phalanx 1, digit 3	1	B	B	A

our study, and we could not check on whether they represent *M. californica* as reported by Howard (1927) and Brodkorb (1964a) or whether they should be referred to as *Meleagris* sp. as suggested by Steadman (1980). It would be especially advisable to check on the presumably well-preserved coracoid, an element that proved to be so useful in our study.

The occurrence of *M. gallopavo* in California has been an issue of some debate in recent

Table 4 Comparison of the characters found on *M. californica*, *M. gallopavo*, and *M. ocellata* with the fossil remains of *M. crassipes* from San Josecito Cave, Mexico. It was possible to check only selected elements and characters because of the relatively low number of specimens available; for the same reason the results are presented as the number of specimens instead of their percentages. "Character #" refers to the numbering of characters used in the main section of this paper. Individual number of specimens of *M. crassipes* whose preservation made it possible to check for our characters are as follows: coracoid LACM/(CIT) 3447, LACM 72072 and 72073; humerus LACM/(CIT) 72074 and 72075, LACM 3443 and 45969, two specimens without numbers; ulna LACM/(CIT) 3444, LACM 45970, 72076, 72077, 72078, three specimens without numbers; carpometacarpus LACM/(CIT) 3445, LACM 72093, 72095, 72096, three specimens without numbers; femur LACM 72081, 72083; tibiotarsus LACM/(CIT) 3448, LACM 45974, 45975, 72086, two specimens without numbers; tarsometatarsus LACM/(CIT) 3449, LACM 4571, 4572, 4573, 72087, 72089, 72090, 72091, six specimens without numbers.

Element	Character # and its typical state	Number of specimens	Character as found in
Coracoid	1:A	2 out of 3	*M. ocellata*
	2:B	2 out of 3	*M. californica*
	3:A	2 out of 3	*M. gallopavo* and *M. ocellata*
	4:A	3 out of 3	*M. gallopavo* and *M. ocellata*
	5:B	3 out of 3	*M. californica*
	6:A	3 out of 3	*M. ocellata*
	7:A	3 out of 3	*M. gallopavo* and *M. ocellata*
Humerus	1:B	6 out of 6	*M. californica*
	2:B	6 out of 6	*M. gallopavo* and *M. californica*
Ulna	1:C	5 out of 8	*M. californica*
Carpometacarpus	1:B	7 out of 7	*M. gallopavo*
Femur	1:B	2 out of 2	*M. gallopavo* and *M. californica*
Tibiotarsus	3:B	5 out of 6	*M. californica*
Tarsometatarsus	1:A	9 out of 14	*M. gallopavo* and *M. ocellata*

decades, largely because of its (re)introduction. Although no unquestionable fossil remains of *M. gallopavo* species have been found in California, we cannot exclude the possibility that this species was once a native resident in California. Based on current evidence, however, we regard this possibility as remote. Nevertheless, a number of late Pleistocene turkey bones from various localities are identified as *Meleagris* sp., and it is likely that even more turkey remains can be found in some of the numerous local collections scattered all over the state. The descriptions of osteological characters presented in this paper, used by one experienced in osteology, might bring to light new discoveries in the future.

SIMILARITIES AND SYSTEMATICS

This section presents the similarities in osteological features among the three species of turkeys central to this study based on characters present on a single element. This analysis is of value mainly for the interpretation of scarce and fragmentary fossil remains from localities with small paleofaunas. Although this is not the case for *Meleagris californica* from Rancho La Brea, specimens of which are abundant and in excellent condition, the information on similarities based on single elements can be useful for interpreting affinities of turkey specimens from other localities where they are known only from a selection of elements. The following comparisons are based on qualitative characters; the species also differ in absolute measurements, but because the average differences in size follow the same pattern in all elements (with *M. gallopavo* being the largest and *M. ocellata* the smallest), they are not included in this analysis.

PREMAXILLA

According to Howard (1928) and Steadman (1980), the premaxilla of *M. californica* is more similar to that of *M. ocellata* than to that of *M. gallopavo*. However, our results show that the fossil species is different from both of the modern taxa, which are more similar to each other than either is to *M. californica*. Contrary to Howard (1928), Steadman (1980) did not consider the differences seen in the premaxillae to be of generic value, and we agree with this interpretation. The differences in the size and shape of the premaxillae can be attributed to probable differences in the diet. That is, the food of *M. californica*, in relatively dry Southern California, was probably somewhat smaller and harder than that of the modern species, which are more at home in more humid forests with more lush vegetation (the present distribution of *M. gallopavo* in more inhospitable areas can be attributed to recent human activities). Therefore, the differences in the premaxillae might reflect adaptations for foraging in different environments.

MANDIBLE

Steadman (1980) noted that *M. gallopavo* differs from *M. ocellata* in characters of the mandible. Our results agree with this. Furthermore, our results show that *M. californica* and *M. ocellata* are indistinguishable by qualitative characters of the mandible, in contrast to the premaxilla. The differences between relative similarities among turkeys obtained from the premaxilla and mandible are perhaps best explained by the fact that different portions of the skull serving different functions are involved in each case (i.e., the tip of premaxilla versus the articular part of the mandible).

QUADRATUM

None of the previous studies included this element. Our results indicate greater similarity of *M. californica* to *M. gallopavo* than to *M. ocellata*.

SKULL

Steadman (1980) did not recognize any differences among the skulls of the three species. Howard (1927) considered the skull of *M. californica* to be more similar to that of *M. ocellata* than to *M. gallopavo*, whereas our results indicate that only *M. ocellata* can be identified with confidence on the basis of the skull.

FURCULA

Howard (1927) regarded *M. californica* as generically distinct from *M. gallopavo* and *M. ocellata*, based on the furcula, but Steadman (1980) questioned the rank of the differences. According to our results, the furcula is one of the most diagnostic elements in turkeys, and the three species have specific characters that permit each to be identified with confidence. In three out of six characters, the furcula of *M. californica* is more similar to that of *M. gallopavo* than to that of *M. ocellata*, and the remaining three characters distinguish it from those of both modern species.

STERNUM

The criteria applied to the sternum by Howard (1927) were inadequate for her to resolve affinities among the turkeys. On the other hand, Steadman (1980) regarded the sternum of *M. californica* as more similar to that of *M. gallopavo* than to that of *M. ocellata*. Our results indicate that the sternum is one of the best elements of turkeys in terms of the number and quality of characters, yet it is hard to say to which of the two modern species *M. californica* is more similar because the fossil taxon shows greater resemblance to one or the other species, depending on the character in question.

CORACOID

According to Steadman (1980:134), "*M. californica* does not consistently differ from *M. gallopavo* or *M. ocellata* in any of the 15 characters [of the coracoid] listed." This contradicted Howard (1927), who regarded *M. californica* as generically separable from *M. gallopavo* and *M. ocellata* based on the coracoid, with a closer resemblance to *M. gallopavo*. Although largely based on different characters, our results can be summarized as being similar to those of Howard (1927), with the exception that we do not give them generic value. As are the furcula and the sternum, the coracoid is one of the most diagnostic elements in turkeys. Its numerous characters form a unique combination that allows all three species to be reliably identified, and, as was shown above on the remains from San Josecito Cave and Howell's Ridge Cave, another combination of the same characters is typical of *M. crassipes*. Therefore, it appears that the same characters of the coracoid, possibly in other combinations, might prove useful for the identification of other fossil turkeys.

SCAPULA

Although Howard (1927) and Steadman (1980) regarded the scapula of *Meleagris californica* to be more similar to that of *M. ocellata* than to that of *M. gallopavo*, they admitted that the conclusion was only a tentative one. Our results, based on one character only, indicate the opposite; that is, there is a greater similarity of the scapula of the fossil species to that of *M. gallopavo* than to that of *M. ocellata*.

HUMERUS

Howard (1927) listed *M. californica* as having a humerus intermediate between *M. gallopavo* and *M. ocellata* in one character and distinct in another. Steadman (1980:135) noted that "the least similarity is between ... *M. gallopavo* and *M. ocellata*. The most similarity is between *M. californica* and *M. crassipes*." Our results generally agree with those of Steadman (1980). *Meleagris ocellata* has the most distinctive humerus, whereas those of *M. californica* and *M. gallopavo* are more similar to each other.

ULNA

According to Howard (1927), the ulna of *M. californica* is more similar to that of *M. ocellata* than to that of *M. gallopavo*. Steadman (1980) considered the ulna to be the least diagnostic element he studied, and he refrained from further comments. Our results indicate a greater similarity of the ulna of *M. californica* to that of *M. gallopavo* than to that of *M. ocellata*, but this is based on one character only. Our second character is species specific.

RADIUS

Howard (1927) found the radius of *M. californica* to be more similar to that of *M. ocellata* than to that of *M. gallopavo*, whereas the results of Steadman (1980) and this study indicate a greater similarity of this element between *M. californica* and *M. gallopavo*.

CARPOMETACARPUS

Howard (1927) found no basis for identifying relationships among turkeys on this element, and Steadman (1980) noted only that *M. ocellata* has the most distinctive carpometacarpus. We agree with those opinions.

PHALANX PROXIMALIS DIGITI MAJORIS

None of the previous studies included this element. Our results indicate that this carpal phalanx of *M. californica* is more similar to that of *M. gallopavo* than to that of *M. ocellata*.

PELVIS AND SYNACRUM

Neither Howard (1927) nor Steadman (1980) found characters on these elements that would help distinguish the three species of turkeys. We also failed to find useful characters, and we excluded these elements from further analysis.

FEMUR

Howard (1927) stated that the femur of *M. californica* is not identical with that of either *M. gallopavo* or *M. ocellata*, and Steadman (1980) noted that *M. ocellata* is least similar to *M. gallopavo* or *M. californica*. We agree with Steadman's (1980) opinion, although our conclusion is based on one character only.

TIBIOTARSUS

The affinities of *M. californica* to *M. gallopavo* or *M. ocellata* based on the tibiotarsus were unclear to Howard (1927) and Steadman (1980), as they are to us.

FIBULA

The fibula of *M. californica* is somewhat different from those of the two other species, and therefore its affinities to them based on this element are unclear (Howard, 1927; Steadman, 1980; present results).

TARSOMETATARSUS

Howard (1927) described five characters for this bone, with the tarsometatarsus of *M. californica* showing a greater resemblance to either that of *M. gallopavo* or *M. ocellata*, depending on the character in question. According to Steadman (1980), the tarsometatarsus is the most diagnostic element in turkeys. Of the 25 characters he described, 18 occurred in all three species, and they showed that this element of *M. californica* is more similar to that of *M. gallopavo* than to that of *M. ocellata*. We found the element more difficult to approach because of large individual variation, and we could find only three valid characters, which revealed more the distinctiveness of *M. californica* than its affinities to either of the modern species.

Many authors (see discussion in Steadman, 1980:137–140) draw systematic conclusions on the basis of the spur of the tarsometatarsus. We are reluctant to describe possible differences in this structure as being of species significance because its development is clearly connected with the age of the bird, and there is no way to know how old our modern and fossil individuals were at the age of their death. Generally, it appears that males of *M. ocellata* have longer and sharper spurs than males of *M. gallopavo*. *Meleagris californica* shows all possible stages of spur development—from a little, porous bump to a well-developed, long spur that seems to be longer than in *M. gallopavo*, but for reasons mentioned above it is difficult to solve the problem definitively. None of the complete female tarsometatarsi of *M. californica* that we sexed by means of scatter plots had any traces of even a rudimentary spur. Still, this does not allow us to state that as far as the presence of the spur in females is concerned, *M. californica* resembles more *M. gallopavo* than *M. ocellata* (whose females are known to have a spur) because, according to Steadman (1980:137), the spur in females of *M. ocellata* is only a slightly elevated scutellum, and its presence is not reflected in any way on the tarsometatarsus.

PES PHALANX 1, DIGIT 3

Our results, based on only one character, indicate that this pedal phalanx of *M. californica* is more similar to that of *M. gallopavo* than to that of *M. ocellata*. The differences in the curvature of the phalanx might be attributable to some adaptations in scratching for food, which is a common behavior in all galliforms. No other studies of comparative turkey osteology have included this element.

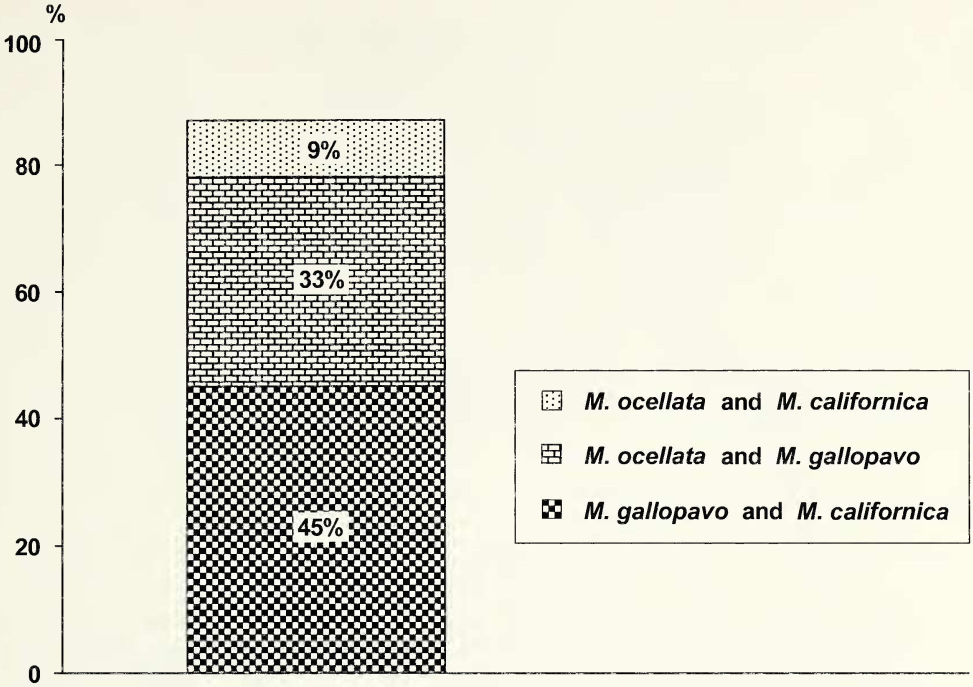


Figure 33 Percentage of characters shared by each pair of species (calculated from all 55 characters described).

DISCUSSION OF SIMILARITIES

The overall similarity between the three species of turkeys, based on all elements studied, can be expressed as the number of characters shared by each pair of species (Fig. 33). From the diagram, it is clear that the extinct species *M. californica* is most similar to the extant species *M. gallopavo*, with which it shares nearly half of all the characters. On the other hand, *M. californica* and *M. ocellata* have very few characters in common, a fact that points to their more distant relationship. The two extant species, *M. gallopavo* and *M. ocellata*, share a moderate number of characters. Although this analysis was based on a different set of characters, the results generally agree with those of Steadman (1980:151), who stated that "*Meleagris californica* is more similar to *M. gallopavo* than to *M. ocellata*..."

The three species also have nearly identical relative lengths of all major long bones of the wing and leg (Fig. 34), which reflects similarities in the structure of their body. Consequently, similar life locomotor habits, in general, including both flying and walking abilities, can be inferred. The small differences between the species are probably negligible because they might be attributable to different sample sizes (*M. californica* most numerous and *M. ocellata* least numerous) and different relative proportions of one sex to the other.

The fact that we did not find any qualitative characters differentiating the five subspecies of *M. gallopavo* supports their present systematic status within a single species, which is based primarily on plumage characteristics. Osteologically, they differ only in average size (Tables A1–A15), although the size range of each subspecies is large and overlaps with those of other subspecies to the extent that it would be difficult to use size to identify the subspecies of an unknown specimen with any reliability (Fig. 35). According to Eaton (1992:3), subspecies of *M. gallopavo* differ in the length of their legs: *M. g. silvestris* and *M. g. merriami* reportedly have a relatively short tarsometatarsus and tibiotarsus, as opposed to *M. g. intermedia* and *M. g. osceola*. Our data do not support Eaton's (1992) conclusion. We analyzed natural logarithms of our original data (separately for tibiotarsus and tarsometatarsus) by means of factorial two-way (subspecies and sex) analysis of variance, followed by Tukey's post hoc test, version for unequal number of observations per group (StatSoft, Inc., 2004). The only statistically significant difference we observed between groups of the same sex but different subspecies was that between the length of tarsometatarsus in females of *M. g. merriami* and females of *M. g. osceola* ($p < 0.01$). We base such conclusions on our material, which, although it is the largest sample studied so far (about 10 specimens from each subspecies), is still a relatively small sample for reliable statistical analysis given the huge sexual and individual size variation in turkeys.

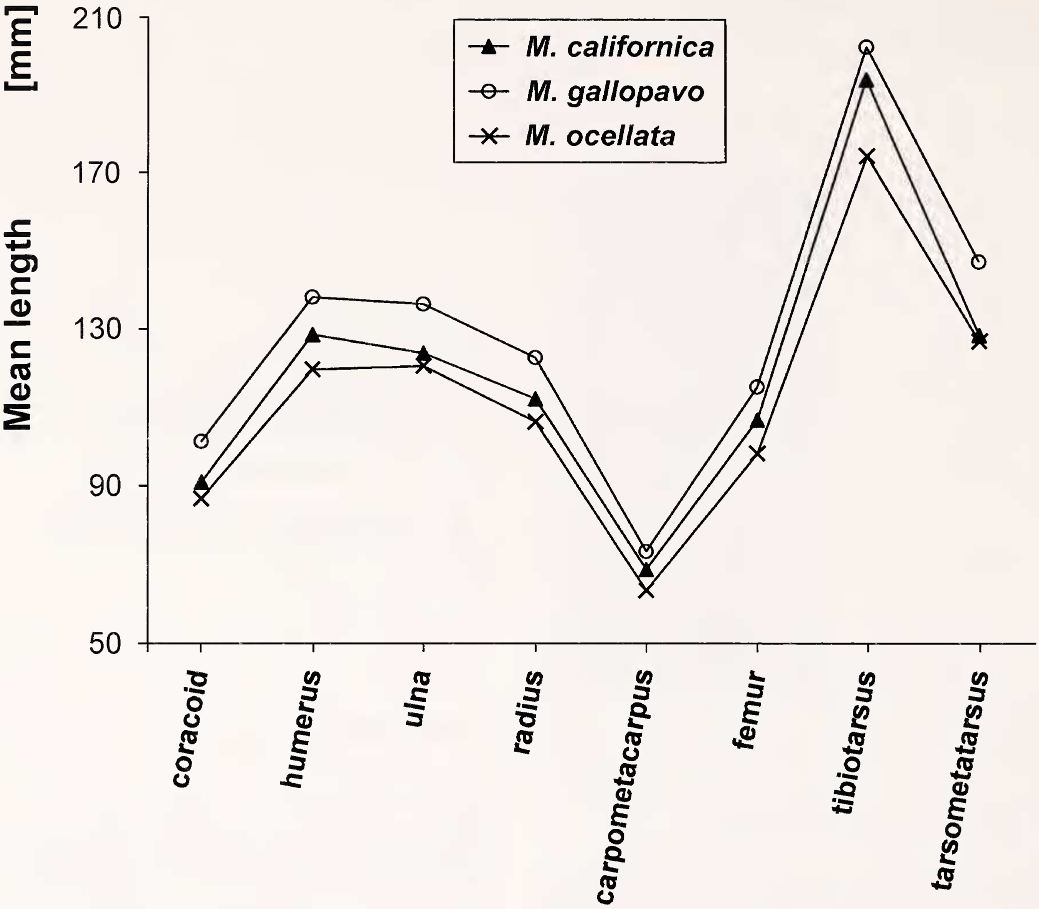


Figure 34 Relative length of major long bones of the wing and leg. "Mean length" refers to arithmetic mean of the total length (Tables A5, A7–A10, A13, A14: measurement A) calculated from all specimens of a particular species (i.e., sexes pooled). Because of frequent damage to the fossil femora, the measurement "total length" was replaced with "medial length" (Table A12: measurement B).

It would be difficult to attribute a level of importance to any particular osteological characters discussed in this study. As mentioned above, most of the characters reflect small differences, and in any species there are nearly always a certain number of "atypical" specimens. Therefore, it seems more likely that the characters represent specific, rather than generic, differences. This, along with the great degree of similarity between *M. californica* and *M. gallopavo*, strongly supports Steadman's (1980) conclusion that the two forms are congeneric and that both should be included in the genus *Meleagris*. Also, Miller and Bowman (1956:44) did not find any grounds for generic separation of the two species on the basis of the tarsometatarsus. On the other hand, our results support only in part Steadman's (1980) conclusion regarding the congeneric affinities of *M. ocellata* and the other two species. The number of characters exclusive to *M. ocellata* indicates that this species is somewhat more removed from *M. gallopavo* and *M. californica* than the latter are from each other. Nevertheless, with our present state of knowledge, which is based on a relatively small sample of specimens, the differences do not seem to justify placing *M. ocellata* in a separate genus. Shufeldt (1914:47), who argued for generic distinction of *M. ocellata* on the basis of its external characters, admitted that the osteological characters he evaluated were of specific rank and wrote, "The skeleton of *Agriocharis* is, bone for bone, character for character, in close agreement with what is presented on the part of the osteology of *Meleagris*." This study, however, indicates that the osteological differences are larger than previously thought. Theoretically, some of these differences might turn out to be of generic rank if it could be demonstrated that certain characters differentiating *M. ocellata* have far-reaching, ecomorphological consequences. This question might be resolvable only through analyses of large comparative collections of *M. ocellata*,

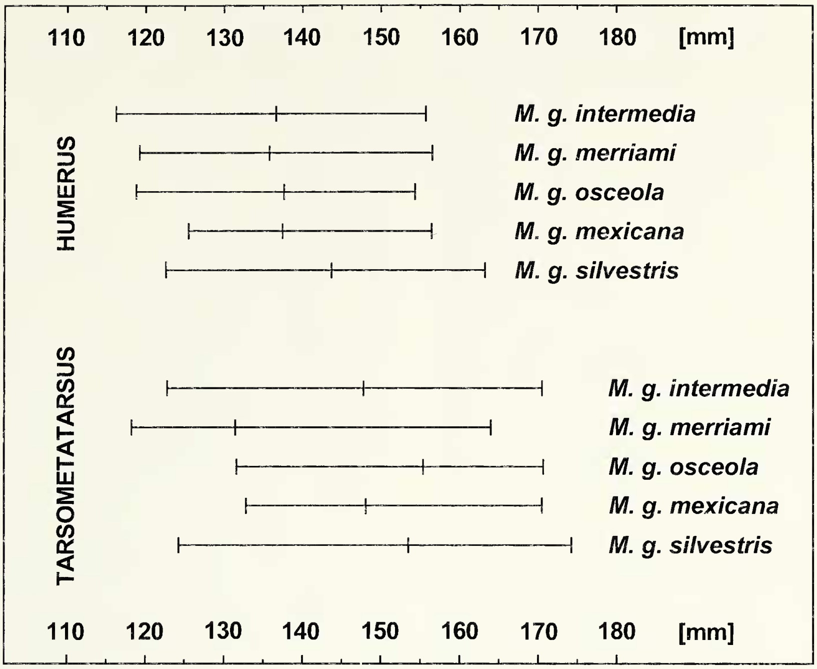


Figure 35 The range (minimum, maximum, and arithmetic mean) of the total length of the humeri and tarsometatarsi in subspecies of *M. gallopavo*. The size ranges within each subspecies largely overlap as well for other bones of the skeleton. Number of specimens for the humerus: *M. g. intermedia*, 9; *M. g. merriami*, 8; *M. g. osceola*, 8; *M. g. mexicana*, 8; *M. g. silvestris*, 10. Number of specimens for the tarsometatarsus: *M. g. intermedia*, 9; *M. g. merriami*, 9; *M. g. osceola*, 8; *M. g. mexicana*, 8; *M. g. silvestris*, 11

which are currently unavailable, and comparative anatomical research.

EVOLUTION

Unfortunately for our overall understanding of the evolution of turkeys, there have been no reports of any significant finds of new fossil turkeys since Steadman's (1980) definitive study. Thus, his discussions remain as our most valuable source for information on the evolution of turkeys, and the relationships of extinct and extant species of turkeys of the southwestern United States, Mexico, and Central America remain unclear.

To briefly summarize the extent of our knowledge, the present geographic distributions of the two extant species [i.e., *M. gallopavo* throughout most of the United States, southern Canada, and northern Mexico; *M. ocellata* in the Yucatán Peninsula and adjoining regions of Mexico and Guatemala (del Hoyo et al., 1994)] do not overlap, and the same is true for the known original geographic ranges of the species (Schorger, 1966). Thus, it can be argued that the two extant species probably were isolated throughout most of the Holocene. The known geographic range of *M. californica* was limited to Southern California, which is very far from that of *M. ocellata*, and it was separated from the known, pre-Columbian range of *M. gallopavo* by the deserts of the southwestern United States (Schorger, 1966; Steadman, 1980).

Our results indicate that geographic isolation and the passage of time resulted in fewer differences between the late Pleistocene *M. californica* and extant *M. gallopavo* than are seen between the two extant species (*M. gallopavo* and *M. ocellata*). Also, as was briefly shown above, osteologically the extinct species *M. crassipes* stands out clearly from the other three species because it shows a mosaic of characters that otherwise typify one or another of the other three species. This might indicate that either *M. ocellata* and *M. crassipes* evolved earlier than *M. californica* and *M. gallopavo* (and therefore had more time to differentiate) or that these two species were exposed to different environmental pressures than the other two taxa. The former possibility would agree with the hypothesis of Griscom (1932), who considered *M. ocellata* to be a relict from a relatively ancient past. Also, Steadman (1980) suggested that *M. ocellata* might have evolved from turkeys that became isolated in the Yucatán region in the middle to late Irvingtonian (middle Pleistocene); at the same time he admitted that the relationship of *M. crassipes* to other turkeys is difficult to assess.

It is possible that different environmental pressures were a mechanism in the speciation of

M. ocellata and *M. crassipes*. Yet it seems less likely that it could be solely responsible for the differences because if differing environmental pressures were a driving force in speciation of turkeys, we would expect to find some qualitative osteological differences among the various subspecies of the widespread CMS 6.39, extant *M. gallopavo*. However, although the subspecies are found in such diverse terrains as the swamps of the southeastern United States, the semiarid mountains of the southwestern United States and northern Mexico (within suitable, localized habitat), and the plains and forests of the northeastern United States (Schorger, 1966), they show no qualitative differences in their skeletal elements. Moreover, we would expect also to see substantial differences in the life habits and natural history of the extant species (*M. gallopavo* and *M. ocellata*), which is apparently not the case (Steadman et al., 1979).

Steadman (1980:154) interpreted the high degree of similarity between *M. californica* and *M. gallopavo* to be a consequence of the fact that either the two species were subjected to similar selective forces after a population of their common ancestors became isolated in California, or that the ancestors of *M. californica* became isolated in California only after reaching the *M. gallopavo* grade. In that our results indicate even greater similarities between the two species than those suggested by Steadman (1980), we are inclined to consider the latter explanation to be more likely. However, without any information on rates of evolution in turkeys, we cannot determine whether the isolation of *M. californica* was a relatively recent phenomenon, and the two species did not have much time to differentiate other than in certain critical features or whether isolation occurred deep in the Pleistocene and slow evolution in these plastic species led to their retaining many similar osteological features. It also could be argued that the isolation was not necessarily complete because intermittent passage through the deserts of the southwestern United Stated might have been possible during particularly wet episodes of the Pleistocene when pluvial lakes covered what are now arid lowlands. On the other hand, the geographic distribution of *M. crassipes* in the southwestern United States is not yet clear. It is possible that this species might have extended its range in such a way at critical times, such as the pluvial periods of the Pleistocene, to intervene between *M. gallopavo* and *M. californica*, thus serving as a factor isolating the latter two species. Only more fossil records will resolve this question.

WHY AN ABUNDANCE OF TURKEYS AT RANCHO LA BREA?

To understand why there are so many turkeys at Rancho La Brea, it is necessary to first understand the basics of entrapment and fossilization in the asphalt seeps. The area comprising Rancho La Brea overlies a large petroleum field from which liquid petroleum seeps to the surface of the ground. This occurs because the area is tectonically active and the overlying rock formations have many faults and fissures through which the petroleum can migrate upward from the petroliferous formations deep underground. Seeps can exist at one location for a substantial period, but they can also quickly disappear from long-term sites and appear at new localities, especially following earthquakes. Once at the surface, as the petroleum spreads laterally over the ground, its more volatile portions dissipate into the air, leaving behind a highly viscous asphalt mix. The areal extent of any given seep is dependent on its longevity, the amount of oil arriving at the ground surface, and the terrain around the seep. Temperature is also a factor because the asphalt ooze will flow farther in hot temperatures than cold. The depth of a seep is not critical for it to be effective as a trap for unsuspecting animals, except perhaps for those mammals of large body size, because the ooze acts like "flypaper," and it is an extremely effective trap, even when present only as a thin layer. For most birds, a step into a fresh seep, regardless of depth, is sure death.

The asphalt seeps do not remain fresh, however, and dust, leaves, and other debris can form a thin "skin," or film, over the surface of a seep. Cold temperatures also can reduce the effectiveness of a seep to entrap animals by solidifying a thin skin on the surface of a seep. In these conditions, an animal would have to be heavy enough, and the seep deep enough, for the bird's foot to sink through the surface skin and into the sticky asphalt below. Thus, an animal could safely traverse a path at some times without risk, but at other times the same route would mean entrapment and death. Death would not be quick; it would come about slowly, probably after many days, and, unless the animal became food for a predator, only by dehydration or starvation. The longer it took for death to occur, the longer the trapped animal would remain attractive to predators seeking live prey. For further details on entrapment in asphalt deposits, see Campbell (1979), Harris and Jefferson (1985), and Stock (2001).

Turkeys are heavy, highly gregarious and social, terrestrial birds. And "the turkey may be expected to behave in certain ways" (Schorger, 1966:161). The basic behavior patterns and life history habits of the extinct California Turkey were probably similar to those of modern turkeys. For details of life history habits of modern turkeys, see Schorger (1966), Eaton (1992), and del Hoyo et al. (1994). We summarize here from those works only those life history aspects that would increase the risk of entrapment of turkeys.

As terrestrial birds, turkeys would be more apt to encounter surface seeps of asphalt than primarily volant birds. Being quite heavy, they would also run a greater risk of breaking through a thin surface film that might cover liquid asphalt should they attempt to walk across a covered seep. Furthermore, turkeys eat primarily vegetable matter, and they have the habit of scratching away surface litter to get at acorns and other nuts, bulbs, and so on. With their heavy bodies, they are very effective at clearing the surface, and if they were to do this while standing on an asphalt seep with a thin layer of covering debris, they would soon find themselves planting their scratching foot with some force into the more sticky ooze below the surface. The result would probably be entrapment.

As gregarious birds with complex social structures, turkeys have a highly developed vocal repertoire. At least 28 different vocalizations are reported for *M. gallopavo* [del Hoyo et al. (1994); detailed in Eaton (1992)]. Vocalizations aid in keeping the flock together, in warning of danger, and even in giving notice of especially good food, among other functions. Once a turkey was trapped in a seep, it would undoubtedly give distress calls, which would bring other members of the flock to see what was the matter. A highly developed sense of curiosity (Schorger, 1966) also would have attracted other members of the flock to the trapped individual, perhaps leading to additional birds being trapped. Furthermore, in optimum habitat conditions, flocks of turkeys can grow to a large size, further increasing the chances that other birds would become entrapped in the asphalt.

This scenario was perhaps even more common with young, inexperienced birds. Unique among the collections of fossil birds from Rancho La Brea, if not collections worldwide, is the large number of immature turkeys, from few-day-old poults to juveniles to young adults. Practically every growth stage of turkeys is represented. Howard (1945) estimated that among the tarsometatarsi, at least 275 of the 750 individuals represented in the collection at that time were less than one year old. Three factors led to this unusual representation of young birds. First, turkeys have large clutches, and nests with 10–12 eggs are fairly common (Eaton, 1992). Large broods lead to increased numbers of individuals subject to entrapment. Second, young birds tend to move about as a tight-knit flock around the hen, and should one become trapped, it is likely that others of the brood would also become trapped as they gathered around the first unfortunate individual. In this instance, the lack of a quick death would lead the brood to remain in the area for some time, increasing the risk of entrapment of additional family members. Turkey broods remain together for several months, which could lead to this scenario taking place at any time in the life of a young turkey. Thus, there was the possibility of a large number of young individuals from a single brood being entrapped during one event or even during multiple events. Third, the bones of immature birds are very soft and porous and do not preserve well under normal processes of fossilization. Preservation in asphalt seeps is not normal, however, and, if not eaten, the carcasses of young turkeys would soon be covered by continued seepage and the accumulation of surface debris. These remains would not have been subjected to wear caused by transport, which is so effective at destroying soft bones. Those bones not covered by asphalt would be lost by destruction by the sun and the weather, but those covered would be fossilized.

In modern turkeys, breeding is cued by photoperiod (del Hoyo et al., 1994), with egg laying in the spring. If true for *M. californica*, this means that young birds were present during the warm summer and fall months, periods when the asphalt seeps were most active and most likely to entrap animals.

It was known that fossil turkeys were uncommonly abundant at Rancho La Brea almost from the beginnings of paleontological excavations at the locality (L. Miller, 1909; Howard, 1927). Only one other avian species is represented by more specimens than the California Turkey, and that is the Golden Eagle, *Aquila chrysaetos* (Howard, 1962b). That these two species are the most abundant is probably not just coincidence but a result of eagle predation on entrapped turkeys.

As noted by Schorger (1966:311), "The golden eagle (*Aquila chrysaetos*) experiences little difficulty in killing an adult wild turkey." Predation on the Wild Turkey by the Golden Eagle was also noted by Lehman and Thompson (2004). Turkeys trapped in the asphalt seeps were probably held fast to the ground by the feet, and they probably struggled to free themselves until exhaustion set in. They were prime targets for the large predatory eagles, which attack on the wing, sinking their talons deep into prey. Unfortunately for the eagles, in many if not most cases, the turkey would not have come free from the asphalt ooze after being seized, and before the eagle could recognize its plight and disengage its talons, it would have experienced a high-speed impact with the ground. A broken neck or other broken bones would have been a predictable outcome. At the least, it could be expected that an eagle would find itself trapped in the asphalt alongside its prey. Of course, the end result for the eagle would be the same if the prey were a turkey or a rabbit, and eagles were probably going after many trapped but still struggling small mammals as well, which probably led to their presence in higher numbers.

EXTINCTION OF *MELEAGRIS CALIFORNICA*

Two aspects of the life histories of turkeys, in combination with an external force, are probably intricately interlinked with their extinction. First, according to Schorger (1966:177), turkeys must drink water every day, and they usually do so twice a day. On the other hand, Eaton (1992:5) says only that they will drink water before and after roosting "if available." Nonetheless, it is clear that in order to survive, a population of turkeys must have a year-round, dependable source of water. For example, in many areas in the semiarid southwestern United States, turkeys survive only because of the presence of livestock watering tanks (del Hoyo et al., 1994), and their movements are limited by water availability (Shaw, 2004). Second, turkeys roost in trees. Thus, they require stands of trees of sufficiently large size for their branches to hold their heavy weight. It is well documented that in areas where forestry practices have led to the removal of large roost trees, turkey populations have suffered (Shaw, 2004). Where trees are absent, they will make use of power poles or windmills (del Hoyo et al., 1994). In the Mediterranean climate of Southern California, both of these requirements (i.e., water and roost trees) can be in abundance or extremely scarce to nonexistent, depending on slight changes in climate. Both are dependent on regional precipitation amounts.

In models of precipitation history of the Los Angeles area for the past 14,000 years, Reid Bryson (personal communication) has shown a dramatic drop to below modern precipitation levels beginning about 11,500 BP (Figs. 36–38). Although these specific graphs have not been published previously, they were derived by use of the tested Macrophysical Climate Model (Bryson, 1992; see also Bryson and Bryson, 2000; Ruter et al., 2004). According to Bryson's model, these dry conditions persisted for hundreds of years, which would have been long enough to dramatically affect vegetation distribution. A similar picture of precipitation history is reported from pollen analysis at Ocean Drilling Project Site 893 in the Santa Barbara Channel, about 160 km west-northwest of Rancho La Brea (Heusser, 1995; Heusser and Sirocko, 1997). Those studies indicate a significant decrease in precipitation levels to near modern levels during the glacial–interglacial transition (~14 to ~11 ka ^{14}CyrBP). The transition is not as abrupt as presented in Bryson's models, but the trend toward a significantly drier climate is similar. We cannot know if these changes in climate, in and of themselves, would have been sufficient to drive the California Turkey to extinction. For example, Johnson (1977a, 1977b) was of the opinion that the climate and habitat changes that took place between the late Pleistocene and the Holocene were probably too small to be the only reason for the mass extinction seen at that time, of which the turkeys were only one species. These climatic changes would, however, certainly have concentrated relictual populations of turkeys to very localized areas. See Stock (2001) for additional general comments on climatic changes at Rancho La Brea.

In a longer-term model of less confidence (Reid Bryson, personal communication), the precipitation chart for Los Angeles shows several periods of even lower rates of precipitation between 39,000 and 35,000 BP (Fig. 39), although the periods of drought were of much shorter duration. The question as to why the California Turkey was able to survive earlier periods of extreme drought and not that at the end of the Pleistocene might be put to the presence of another critical external factor, which was the arrival of paleoindians.

The presence of paleoindians on the west coast of North America by 12,000 BP is now well documented (e.g., Stenger, 2002). When you combine the fact that turkey populations might have been severely reduced in number and concentrated around a few sources of drinking water and roost trees following the end of the Pleistocene climate change with the arrival of hunters who also would have been drawn to sources of freshwater, it is reasonable to predict that the hunters could have driven this highly desirable food species to extinction in a short period of time. When highly localized populations of turkeys, with their great natural curiosity and no fear of humans, were encountered by paleoindians, the outcome was probably inevitable. In other parts of North America, turkeys were hunted and used for all possible purposes by the indigenous peoples, and there is an immense pool of data documenting this use of turkeys (e.g., Schorger, 1966). Although we do not have any direct evidence of human/turkey interactions in California from the boundary between the late Pleistocene and the Holocene, this is one instance where all indicators suggest that a species might have been driven to extinction at the end of the Pleistocene by early hunters. The more wide-ranging *M. gallopavo* would not have experienced the same pressures, except perhaps on local scales.

SUMMARY

A review of all collections of fossil birds from Rancho La Brea housed at the George C. Page Museum revealed about 2,000 additional specimens of *M. californica* that were not recognized as turkeys before. Thus, the total number of turkey specimens increased from about 9,000 to 11,116, representing a minimum of 791 individuals. All of the fossil turkey bones were included in this study, with the exception of some minor elements (e.g., most wing and toe phalanges, vertebrae, and ribs), heavily damaged bones, and young, incompletely ossified specimens.

A comparative osteology of turkeys, including the extinct *M. californica* and both extant turkeys, *M. gallopavo* and *M. ocellata*, was

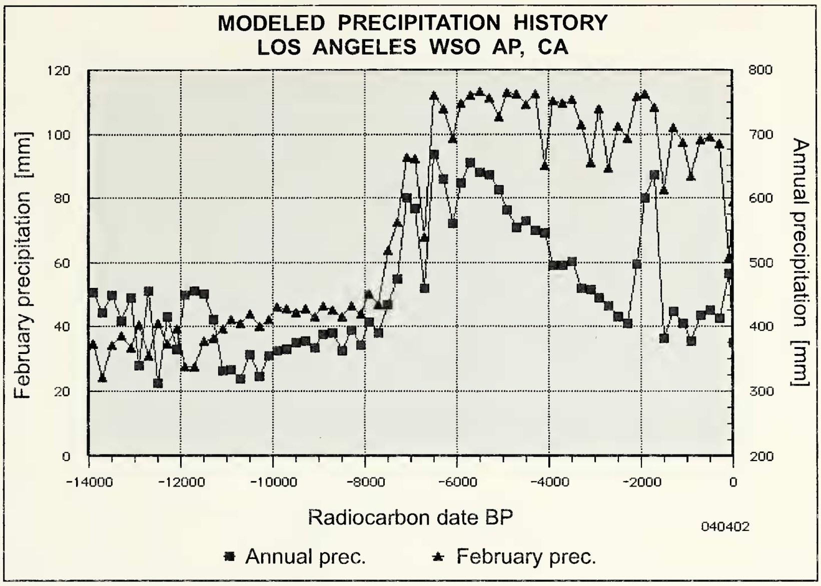


Figure 36 Model of precipitation history (annual *vs.* February precipitation) of the Los Angeles area for the past 14,000 years (Reid Bryson, personal communication). About 11,500 BP, a dramatic drop to below modern precipitations levels began. These dry conditions are postulated to have persisted for hundreds of years, which would have dramatically affected vegetation distribution.

undertaken. Of the 55 qualitative characters described, more than half were located on the head (premaxilla, mandible, skull, and quadratum), the sternum, and parts of the shoulder girdle (furculum, coracoid), which appeared to be the most diagnostic elements. The characters are sufficient to differentiate the three species or to eliminate one of them, depending on the bone. Most of the characters were typical of *M. ocellata* (25) and *M. californica* (18), and only five were characteristic exclusively of *M. gallopavo.* The numerous measurements taken from each of the

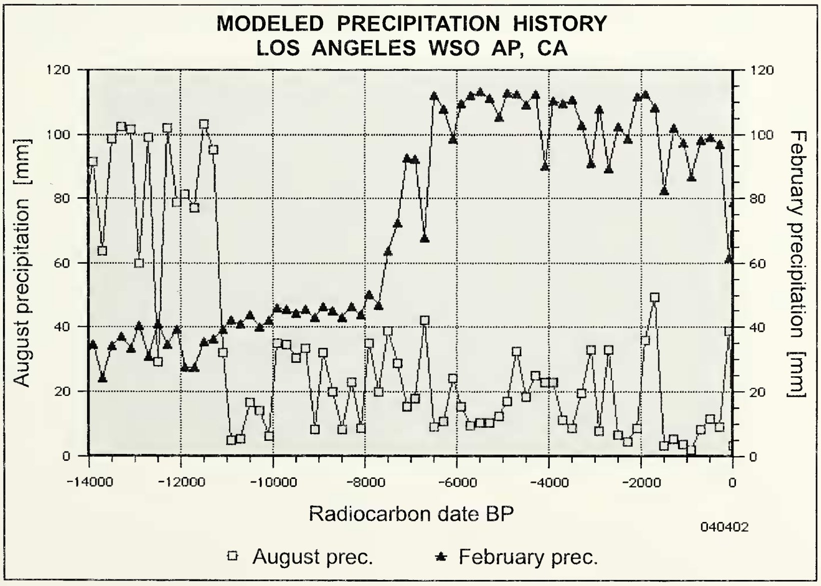


Figure 37 Model of precipitation frequency history (August *vs.* February) of the Los Angeles area for the past 14,000 years (Reid Bryson, personal communication). At about 11,500 BP, a dramatic drop in the frequency of precipitation days in August is postulated.

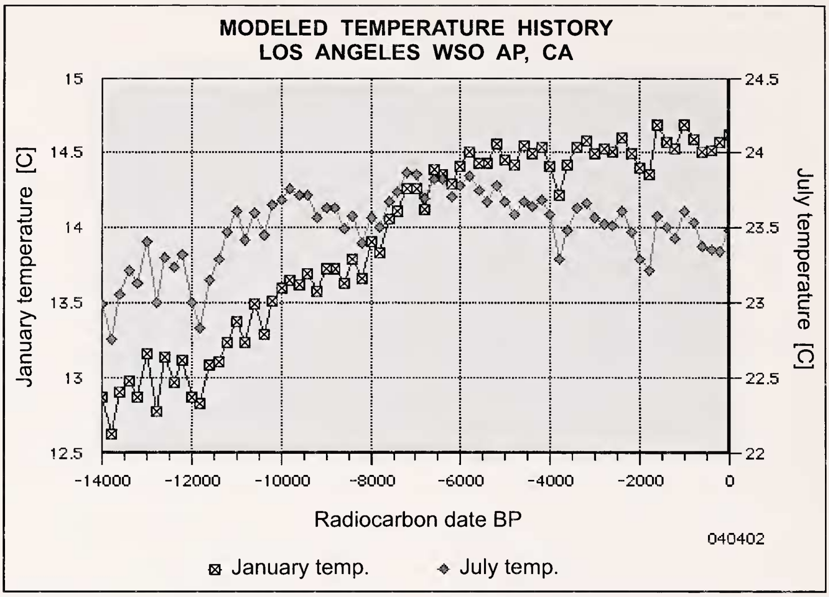


Figure 38 Model of temperature history (January *vs.* July) of the Los Angeles area for the past 14,000 years (Reid Bryson, personal communication). After a low point just after 12,000 BP, the temperatures began to rise toward modern levels, which would have compounded the affects of reduced annual precipitation.

elements made it possible to define the size ranges of particular species, subspecies, and sexes. Sexual size dimorphism in *M. gallopavo* and *M. californica* was examined in detail, and the sex ratio in *M. californica* was tentatively evaluated as being 1:1.

A close similarity between *M. californica* and *M. gallopavo* suggests that the fossil species is more closely related to *M. gallopavo* than to *M. ocellata* and that the ancestors of *M. californica* became isolated in California only after nearly reaching the *M. gallopavo* grade. The large number of turkeys fossilized at Rancho La Brea is linked to the peculiar entrapment characteristics of the asphalt seeps and the gregarious social behavior of these large terrestrial birds. It is postulated that the extinction of *M. californica* was the result of a combination of two factors: a dramatic drop of precipitation to below modern precipitation levels beginning about 11,500 BP, which concentrated the birds around scarce sources of water and limited roost sites, and the arrival of paleoindians in California, who might have hunted to extinction the concentrated birds.

Fossil turkey remains from all other localities maintained in the Vertebrate Paleontology Section of the Natural History Museum of Los Angeles County were checked for the qualitative characters found on the three main species investigated. This survey allowed us to verify the species identification and the known range of *M. californica* and *M. crassipes*. It confirmed the presence of *M. californica* in California within a relatively small range extending from Orange County in the south (Imperial Highway), through Los Angeles County (Rancho La Brea and probably also Workman and Alhambra Streets), to Santa Barbara County in the north (Carpinteria). Moreover, a unique combination of characters allowed us to confirm the presence of *M. crassipes* in Howell's Ridge Cave, Grant County, New Mexico, which indicates that its range extended from northeastern Mexico (San Josecito Cave) to at least New Mexico during the late Pleistocene.

ACKNOWLEDGMENTS

This project was sponsored by the National Wild Turkey Federation (NWTF) and the Natural History Museum of Los Angeles County. We thank Kimball L. Garrett and Christina Couroux, from the Natural History Museum of Los Angeles County, for preparing the specimens of *M. gallopavo* supplied by the NWTF. We also thank the following curators for making available modern comparative specimens: Kathy C. Molina, Dickey Collection at the University of California, Los Angeles; Carla Cicero, Museum of Vertebrate Zoology, University of California, Berkeley; Philip P. Unitt, San Diego Natural History Museum; and Robert Payne and Janet Hinshaw, Museum of Zoology, University of Michigan. Our cordial thanks go to Reid Bryson for sharing with us his unpublished data on the precipitation history of the Los Angeles region and to Tommy Tyrberg for giving us access to his unpublished checklist of the fossil turkey remains. We are also grateful to Bartosz Jenner for his help in the statistical analyses and to the staff and volunteers of the George C. Page Museum, who were invaluable in gathering together and preparing the extremely numerous avian specimens at Rancho La Brea. Four of these individuals,

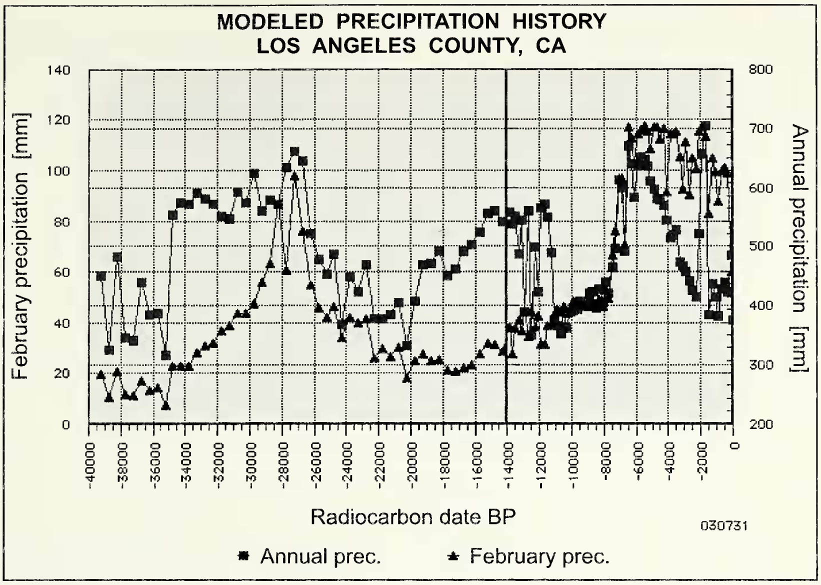


Figure 39 Model of precipitation history (annual *vs.* February precipitation) of the Los Angeles area for the past 40,000 years (Reid Bryson, personal communication). Several periods of low rates of precipitation are postulated between 40,000 and 35,000 BP, but they were of shorter duration, albeit more intense, than the longer dry period that began about 11,500 BP.

Shelley Cox, Karine Pezeril, Judy Scharf, and Christopher A. Shaw, were particularly helpful in various and many ways during the project and made life for Zbigniew M. Bocheński and his family much easier and more pleasant during their stay in Los Angeles. Zbigniew M. Bocheński is also very grateful to Alicja and Józef Lądowicz of Los Angeles and to Elizabeth and Jan Szupiński of Santa Monica and their families for their invaluable help and Polish hospitality during the one-year project. Finally, we thank the reviewers of the manuscript, Per Ericson, John M. Harris, David Steadman, and Tommy Tyrberg, for their valuable detailed comments.

LITERATURE CITED

Baumel, J.J., A.S. King, A.M. Lucas, J.E. Breazile, and H.E. Evans (eds). 1979. *Nomina Anatomica Avium.* London: Academic Press, 637 pp.

Baumel, J.J., A.S. King, A.M. Lucas, J.E. Breazile, H.E. Evans, and J.C. Vanden Berge (eds). 1993. *Nomina Anatomica Avium.* Publications of the Nuttall Ornithological Club, no. 23: i–xxiv, 1–779.

Bocheński, Z.M. 1994. The comparative osteology of grebes (Aves: Podicipediformes) and its systematic implications. *Acta zoologica cracoviensia* 37(1): 191–346.

———. 2005. Owls, diurnal raptors and humans: Signatures on avian bones. In *Biosphere to lithosphere: New studies in vertebrate taphonomy*, ed. T. O'Connor, 31–45. Oxford: Oxbow Books.

Bocheński, Z.M., and K.E. Campbell, Jr. 2005. The identification of turkey remains to species—A metrical approach. In *Feathers, grit and symbolism: Birds and humans in the Old and New Worlds*, ed. G. Grupe and J. Peters, 19–25. *Documenta Archaeobiologiae,* vol. 3. Rahden/Westfalen: Verlag Marie Leidorf GmbH.

Brodkorb, P. 1964a. Catalogue of fossil birds: Part 2 (Anseriformes through Galliformes). *Bulletin of the Florida State Museum, Biological Sciences* 8(3):195–335.

———. 1964b. Notes on fossil turkeys. *Quarterly Journal of the Florida Academy of Sciences* 27(3):223–229.

Bryson, R.A. 1992. A macrophysical model of the Holocene intertropical convergence and jetstream positions and rainfall for the Saharan region. *Meteorological and Atmospheric Physics* 47: 247–258.

Bryson, R.A., and R.U. Bryson. 2000. Site-specific high-resolution models of the monsoon for Africa and Asia. *Global and Planetary Change* 26:77–84.

Campbell, K.E., Jr. 1979. The non-passerine Pleistocene avifauna of the Talara Tar Seeps, northwestern Peru. *Royal Ontario Museum, Life Sciences Contributions* 118:1–203.

Chapman, F.M. 1896. Notes on birds observed in Yucatán. *Bulletin of the American Museum of Natural History* 8(18):271–290.

Cuvier, G. 1820. *Mémoires du Muséum d'Histoire naturelle* 6:1–4.

Eaton, S.W. 1992. Wild turkey. In *The Birds of North America,* no. 22, ed. A. Poole, P. Stettenheim, and F. Gill, 1–27. Philadelphia: The Academy of Natural Sciences.

Gheţie, V., Şt. Chiţescu, V. Coţofan, and A. Hillebrand. 1976. *Anatomical atlas of domestic birds.* Bucureşti: Editura Academiei Republicii Socialiste România, 294 pp.

Griscom, L. 1932. The distribution of bird-life in Guatemala. *Bulletin of the American Museum of Natural History* 64:1–439.

Harris, J.M., and G.T. Jefferson (eds). 1985. *Treasures of the Tar Pits*. Los Angeles: Natural History Museum of Los Angeles County, 87 pp.

Heusser, L.E. 1995. Pollen stratigraphy and paleoecologic interpretation of the last 160 kyr from Santa Barbara Basin, Ocean Drilling Project Hole 893A. In *Proceedings of the Ocean Drilling Program, Scientific Results* 146(2):265–279. College Station, Texas: Ocean Drilling Program.

Heusser, L.E., and F. Sirocko. 1997. Millennial pulsing of environmental change in southern California from the past 24 k.y: A record of Indo-Pacific ENSO events? *Geology* 25(3):243–246.

Howard, H. 1927. A review of the fossil bird, *Parapavo californicus* (Miller), from the Pleistocene asphalt beds of Rancho La Brea. *University of California Publications in Geological Sciences* 17(1):1–56.

———. 1928. The beak of *Parapavo californicus* (Miller). *Bulletin of the Southern California Academy of Sciences* 27(3):90–91.

———. 1936. A new record for *Parapavo californicus* (Miller). *Condor* 38(6):249–250.

———. 1945. Observations on young tarsometatarsi of the fossil turkey *Parapavo californicus* (Miller). *The Auk* 62:596–603.

———. 1962a. Bird remains from a prehistoric cave deposit in Grant County, New Mexico. *Condor* 64(3):241–250.

———. 1962b. A comparison of avian assemblages from individual pits at Rancho La Brea, California. *Contributions in Science, Natural History Museum of Los Angeles County* 58:1–24.

———. 1963. Fossil birds from the Anza-Borrego Desert. *Contributions in Science, Natural History Museum of Los Angeles County* 73:1–33.

———. 1980. Illustrations of avian osteology taken from "The avifauna of Emeryville Shellmound." *Contributions in Science, Natural History Museum of Los Angeles County* 330:xxvii–xxxviii.

Howard, H., and A.H. Miller. 1933. Bird remains from cave deposits in New Mexico. *Condor* 35(1): 15–18.

del Hoyo, J., A. Elliott, and J. Sargatal (eds). 1994. *Handbook of the Birds of the World,* vol. 2. Barcelona: Lynx Edicions, 638 pp.

Johnson, D.L. 1977a. The California Ice-Age refugium and the Rancholabrean extinction problem. *Quaternary Research* 8:149–153.

———. 1977b. The late Quaternary climate of coastal California: Evidence for an Ice Age refugium. *Quaternary Research* 8:154–179.

Lehman, C.P., and D.J. Thompson. 2004. Golden Eagle (*Aquila chrysaetos*) predation attempts on Merriam's turkeys (*Meleagris gallopavo merriami*) in the southern Black Hills, South Dakota. *Journal of Raptor Research* 38(2):192.

Marcus, L.F., and R. Berger. 1984. The significance of radiocarbon dates from Rancho La Brea. In *Quaternary extinctions: A prehistoric revolution*, ed. P.S. Martin and R.G. Klein, 159–183. Tucson: University of Arizona Press.

Martin, L.D., and J. Tate. 1970. A new turkey from the Pliocene of Nebraska. *Wilson Bulletin* 82(2): 214–218.

Miller, A.H., and R. Bowman. 1956. Fossil birds of the Late Pliocene of Cita Canyon, Texas. *Wilson Bulletin* 68(1):38–46.

Miller, L., and C.S. Johnstone. 1937. A Pliocene record of *Parapavo* from Texas. *Condor* 39(5):229.

Miller, L.H. 1909. *Pavo californicus*, a fossil peacock from the Quaternary asphalt beds of Rancho La Brea. *University of California Publications, Bulletin of the Department of Geology* 5(19):285–289.

———. 1911. Avifauna of the Pleistocene cave deposits of California. *University of California Publications, Bulletin of the Department of Geology* 6(16):385–400.

———. 1916. A review of the species *Pavo californicus. University of California Publications, Bulletin of the Department of Geology* 9(7):89–96.

———. 1925. The birds of Rancho La Brea. *Carnegie Institution of Washington Publication* 349: 63–106.

———. 1927. The finding of Pleistocene material in an asphalt pit at Carpinteria, California: Bird remains. *Science* 66(1702):156.

———. 1940. A new Pleistocene turkey from Mexico. *Condor* 42(3):154–156.

———. 1942. A new fossil bird locality. *Condor* 44(6):283–284.

Miller, W.E. 1971. Pleistocene vertebrates of the Los Angeles Basin and vicinity (exclusive of Rancho La Brea). *Bulletin of the Los Angeles County Museum of Natural History* 10:1–124.

Rea, A.M. 1980. Late Pleistocene and Holocene turkeys in the Southwest. *Contributions in Science, Natural History Museum of Los Angeles County* 330: 209–224.

Ruter, A., J. Arzt, S. Vavrus, R.A. Bryson, and J.E. Kutzbach. 2004. Climate and environment of the subtropical and tropical Americas (NH) in the mid-Holocene: Comparison of observations with climate model simulations. *Quaternary Science Reviews* 23:663–679.

Schorger, A.W. 1966. *The Wild Turkey: Its history and domestication*. Norman: University of Oklahoma Press, 625 pp.

Shaw, H. 2004. *Stalking the big bird*. Tucson: University of Arizona Press, 141 pp.

Shufeldt, R.W. 1914. On the skeleton of the Ocellated Turkey (*Agriocharis ocellata*), with notes on the osteology of other Meleagrididae. *Aquila* 21:1–52 + 14 plates.

StatSoft, Inc. 2004. *Electronic statistics textbook*. Tulsa, Oklahoma: StatSoft. Available at http://www.statsoft.com/textbook/stathome.html.

Steadman, D.W. 1980. A review of the osteology and paleontology of turkeys (Aves: Meleagridinae). *Contributions in Science, Natural History Museum of Los Angeles County* 330:131–207.

Steadman, D.W., J. Stull, and S.T. Eaton. 1979. Natural history of the Ocellated Turkey. *World Pheasant Association Journal* 4:15–37.

Stenger, A.T. 2002. Temporal association of paleontological and archaeological resources in Woodburn, ca. 12,000 BP: A preliminary report. *Current Archaeological Happenings in Oregon* 27(3/4): 12–17.

Stock, C. (Revised by J.H. Harris). 2001. Rancho La Brea: A record of Pleistocene life in California. *Natural History Museum of Los Angeles County, Science Series* 37:1–113.

Sushkin, P.P. 1928. On the affinities of *Parapavo californicus* (Loye Miller). *Ibis, 12th Series* 4(1): 135–138.

Tomek, T., and Z.M. Bocheński. 2000. *The comparative osteology of European corvids (Aves: Corvidae), with a key to the identification of their* *skeletal elements*. Kraków: Publications of the Institute of Systematics and Evolution of Animals, 102 pp.

Wetmore, A. 1924. Fossil birds from southeastern Arizona. *Proceedings of the United States National Museum* 64(5):1–18.

———. 1931. The fossil birds of North America. In *Check-list of North American birds*, 4th ed., 401–472. Lancaster, Pennsylvania: American Ornithologists' Union.

Received 29 April 2005; accepted 7 December 2005.

APPENDICES

Illustrations of measurements taken (Figures A1–A7) and tables of mensural data (Tables A1–A15)

The measurements taken are illustrated in Figures A1–A7. In the tables, elements are listed in anatomical order, starting with the head and the sternum, followed by the wing and leg bones. Each element begins with *Meleagris californica*, followed by *Meleagris ocellata* and *Meleagris gallopavo*. Complete specimens of *M. californica* were sexed by plotting their total length against one of the other measurements (i.e., depth or width). As explained in the text, two clearly separated groups of individuals appear in plots of mensural data (see Figs. 29–32). Thus, we felt justified in identifying the smaller group as females and the larger group as males. Although it would be possible to apply that procedure to all elements, we did so only in the cases where bones were numerous (sternum and all the postcranial elements); the limited data for the head (premaxilla, mandible and cranium) would not be representative if split into the sexes. In the case of *M. gallopavo*, the data are presented for all specimens of the species (i.e., with all subspecies and sexes pooled), for each sex separately (subspecies pooled), and for each subspecies separately (sexes pooled).

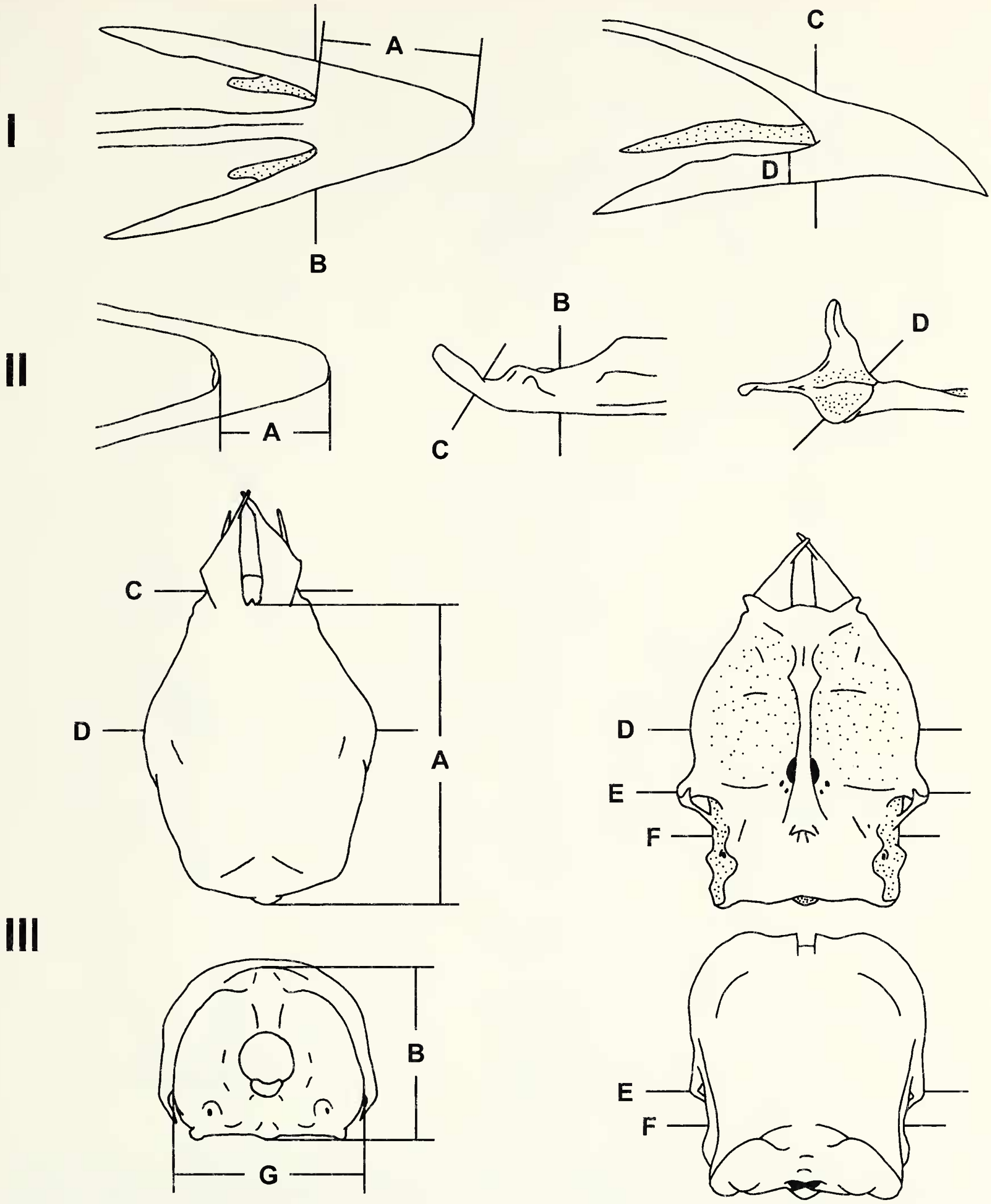


Figure A1 I. Premaxilla: measurements (refer to Table A1). A, length of Os premaxillare, measured between Apex premaxillaris and the anterior end of Apertura nasi ossea (external nares); B, bill width, measured at the anterior end of external nares; C, bill height, measured at the anterior end of external nares; D, width of Processus maxillaris, measured in plane of the bone. II. Mandible: measurements (refer to Table A2). A, length of Pars symphysialis; B, depth of Ramus mandibulae, measured adjacent to the Fossa articularis quadratica; C, depth of Processus caudalis, measured at its shallowest portion, adjacent to the Fossa articularis quadratica; D, maximum diagonal width of the Fossa articularis quadratica. III. Skull: measurements (refer to Table A3). A, total length, measured between Prominentia cerebellaris and the base of the Os nasale; B, height of skull, measured between Lamina parasphenoidalis (basitemporal plate) and Os parietale; C, minimum frontal width of skull, measured at the base of the Os nasale; D, maximum frontal width of skull, measured adjacent to Processus postorbitalis; E, distance between the ventral ends of left and right Processus postorbitalis; F, parietal width of skull, measured between Processus postorbitalis and Processus temporalis; G, width of skull through the occipital region

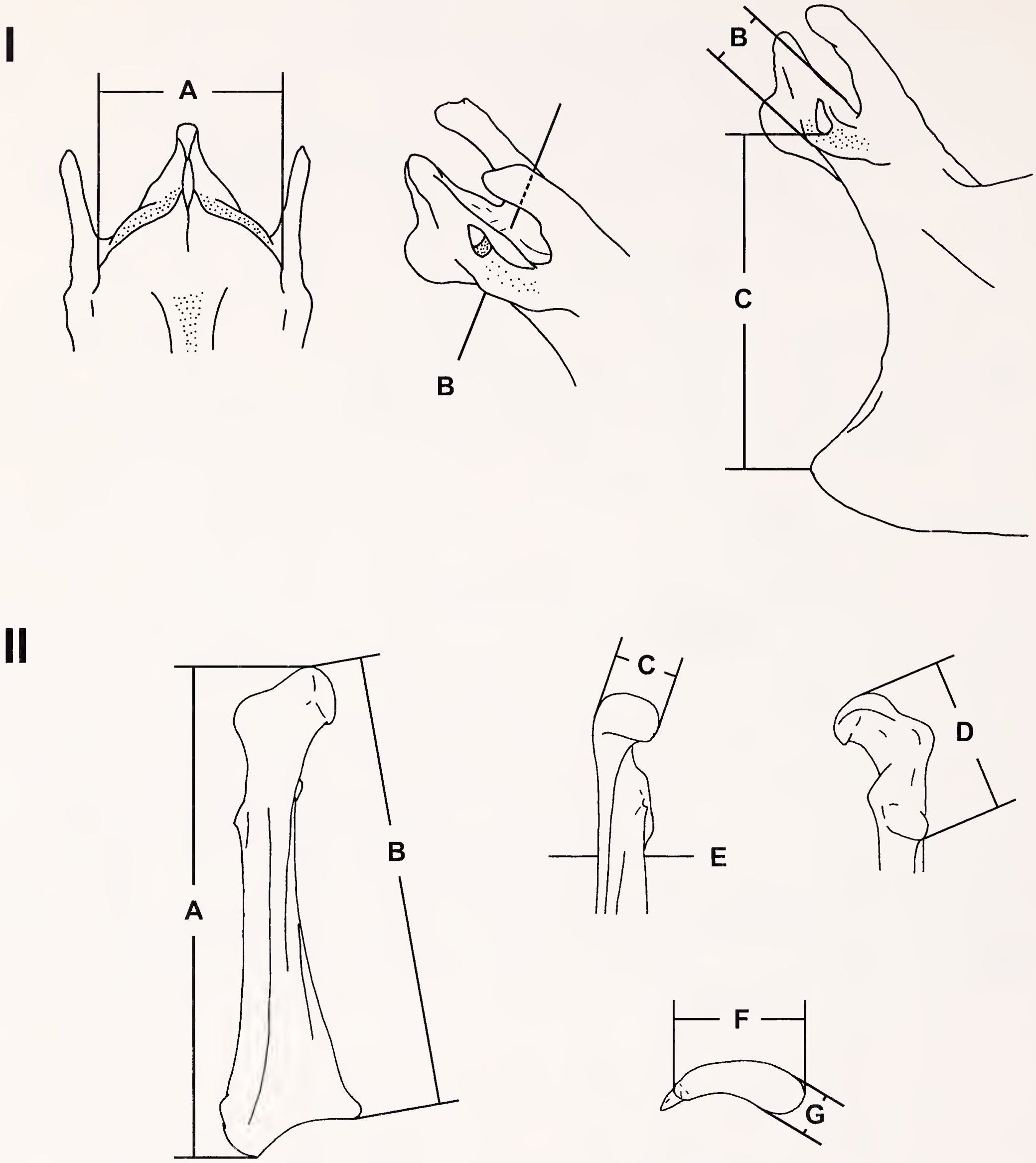


Figure A2 I. Sternum: measurements (refer to Table A4). A, width through Labri ventrale; B, distance between Labrum ventrale and Labrum dorsale, measured adjacent to Rostrum sterni, with calipers flat against ventral side of Labrum ventrale and dorsal side (i.e., not the edge) of Labrum dorsale; C, height of Crista sterni, measured between Apex carinae and the dorsal side of Labrum ventrale (in specimens with an ill-defined, rounded Apex carinae, calipers were placed against most anterior point). II. Coracoid: measurements (refer to Table A5). A, total length, measured between Processus acrocoracoideus and Angulus lateralis; B, medial length, measured between Processus acrocoracoideus and Angulus medialis; C, width of Facies articularis clavicularis; D, height of cranial end, measured between Processus acrocoracoideus and Cotyla scapularis; E, anteroposterior depth of shaft, measured below Cotyla scapularis, with posterior side flat against the calipers; F, sternal width, measured between Angulus medialis and the lateral edge of Angulus lateralis; G, sternal depth, measured at the medial end

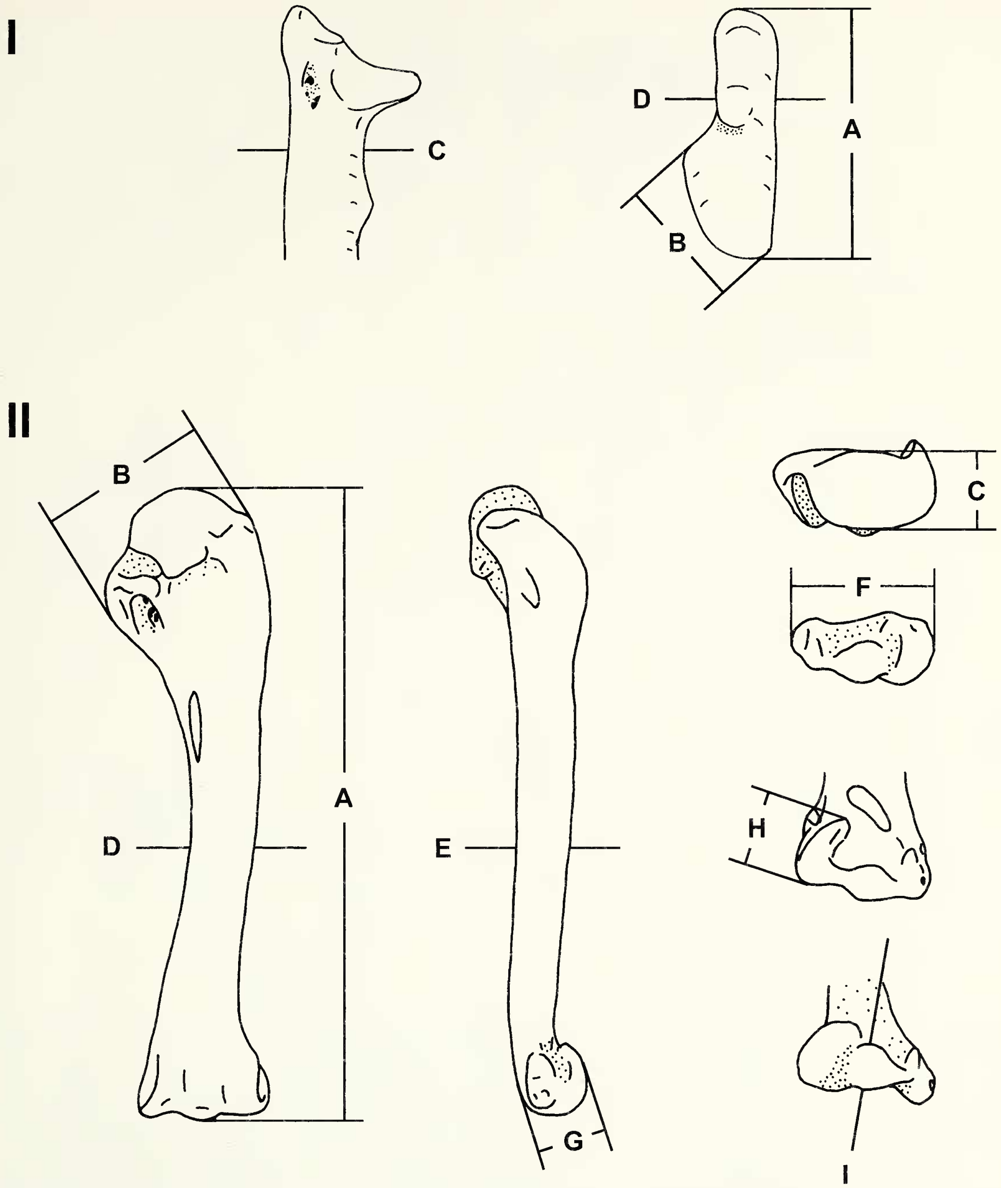


Figure A3 I. Scapula: measurements (refer to Table A6). A, maximum articular length; B, length of Facies articularis humeralis; C, width of shaft, measured between articular end and Tuberculum m. scapulotricipitis; D, width of Tuberculum coracoideum. II. Humerus: measurements (refer to Table A7). A, total length, measured between Caput humeri and Condylus ventralis; B, proximal width; C, proximal depth; D, width at midshaft; E, depth at midshaft; F, distal width; G, depth of Condylus dorsalis, with calipers flat against the ridge on the posterior side; H, height of Condylus dorsalis; I, maximum diameter of Condylus ventralis

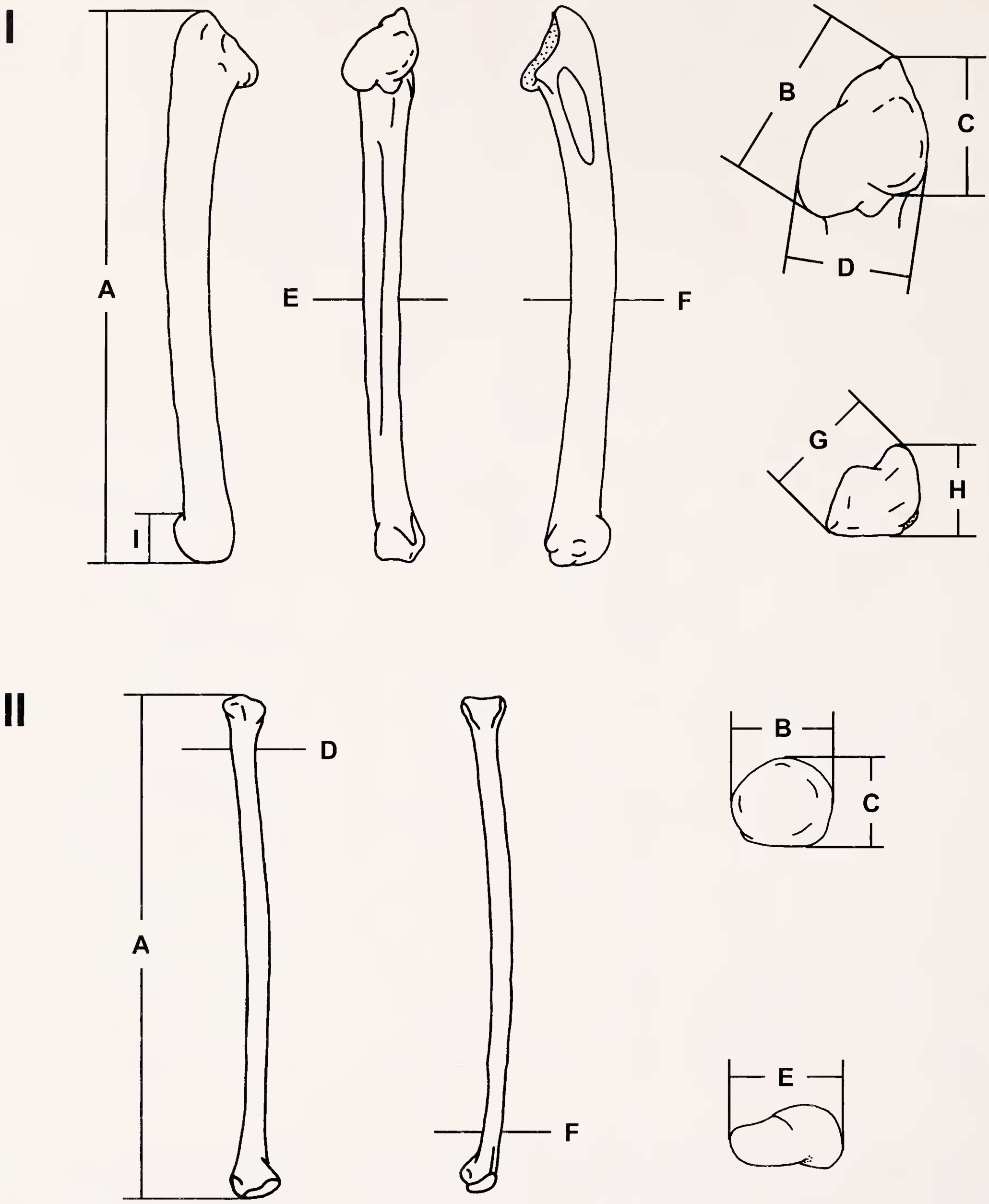


Figure A4 I. Ulna: measurements (refer to Table A8). A, total length, measured between Olecranon and Condylus dorsalis; B, diagonal proximal height; C, height of Cotyla ventralis; D, proximal width; E, minimum diameter at midshaft; F, maximum diameter at midshaft; G, diagonal distal width; H, depth of Condylus dorsalis; I, length of Condylus dorsalis. II. Radius: measurements (refer to Table A9). A, total length, measured between the posterior rim of the proximal end and Facies articularis radiocarpalis; B, maximum proximal width; C, minimum proximal width; D, minimum width of shaft near proximal end; E, distal width; F, minimum depth of shaft near distal end

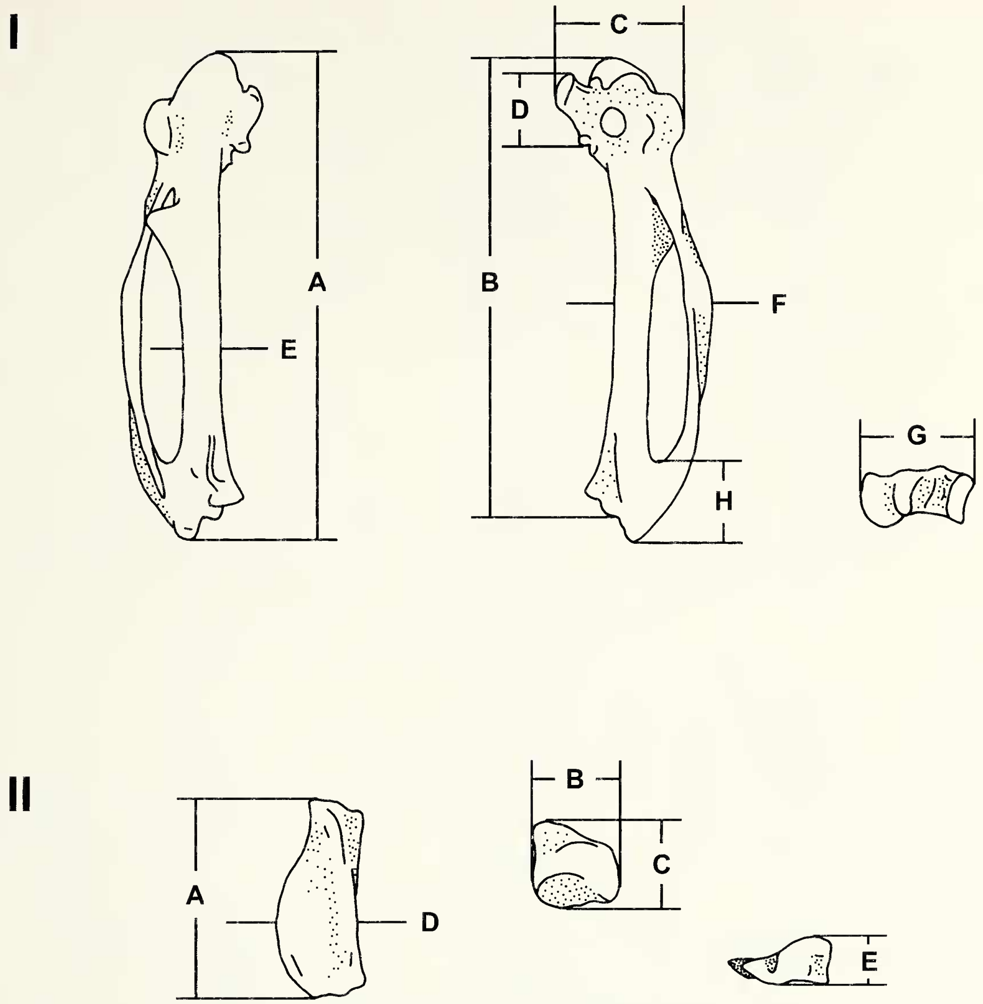


Figure A5 I. Carpometacarpus: measurements (refer to Table A10). A, total length; B, anterior length; C, proximal width; D, length of Os metacarpale alulare; E, width of Os metacarpale majus, measured at midpoint between the proximal edge of Symphysis metacarpalis distalis and the tip of Processus intermetacarpalis; F, midwidth of carpometacarpus, measured at the bulging on Os metacarpale minus; G, distal width; H, length of Symphysis metacarpalis distalis. II. Phalanx proximalis digiti majoris: measurements (refer to Table A11). A, total length; B, proximal depth, measured with the ventral side flat against the calipers; C, proximal width, measured with the ventral side parallel to the "handle" of the calipers; D, maximum width of bone, measured with the anterior side flat against the calipers; E, distal depth, measured with the ventral side flat against the calipers

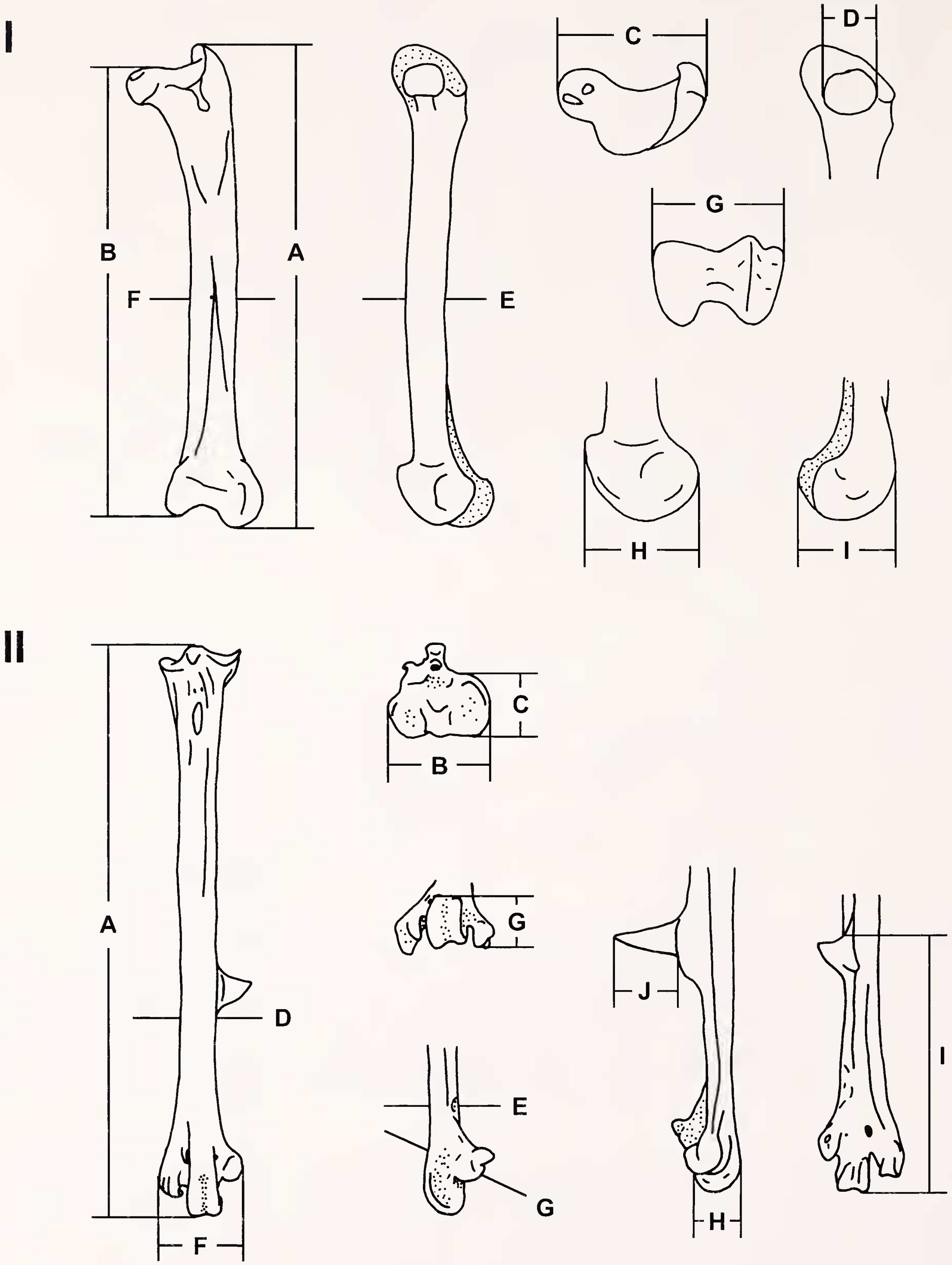


Figure A6 I. Femur: measurements (refer to Table A12). A, total length, measured between Trochlea femoris and Condylus lateralis; B, medial length, measured between Caput femoris and Condylus medialis; C, proximal width, measured between Caput femoris and Trochanter femoris; D, width of Caput femoris; E, minimum diameter at midshaft; F, maximum diameter at midshaft; G, distal width, measured between Condylus medialis and the Trochlea fibularis; H, depth of Condylus medialis; I, depth of Condylus lateralis through Crista tibiofibularis. II. Tarsometatarsus: measurements (refer to Table A14). A, total length, measured between Eminentia intercondylaris and the lateral side of Trochlea metatarsi III; B, proximal width; C, depth of Cotyla medialis; D, minimum (i.e., mediolateral) width of shaft, measured at about one-third of its length from distal end; E, minimum depth of shaft, measured at Fossa metatarsi I; F, distal width; G, distance between dorsal surface of the base of Trochlea metatarsi III and plantar side of Trochlea metatarsi II; H, depth of lateral side of Trochlea metatarsi III; I, proximal side of base of spur core to the lateral end of Trochlea metatarsi III; J, length of spur core

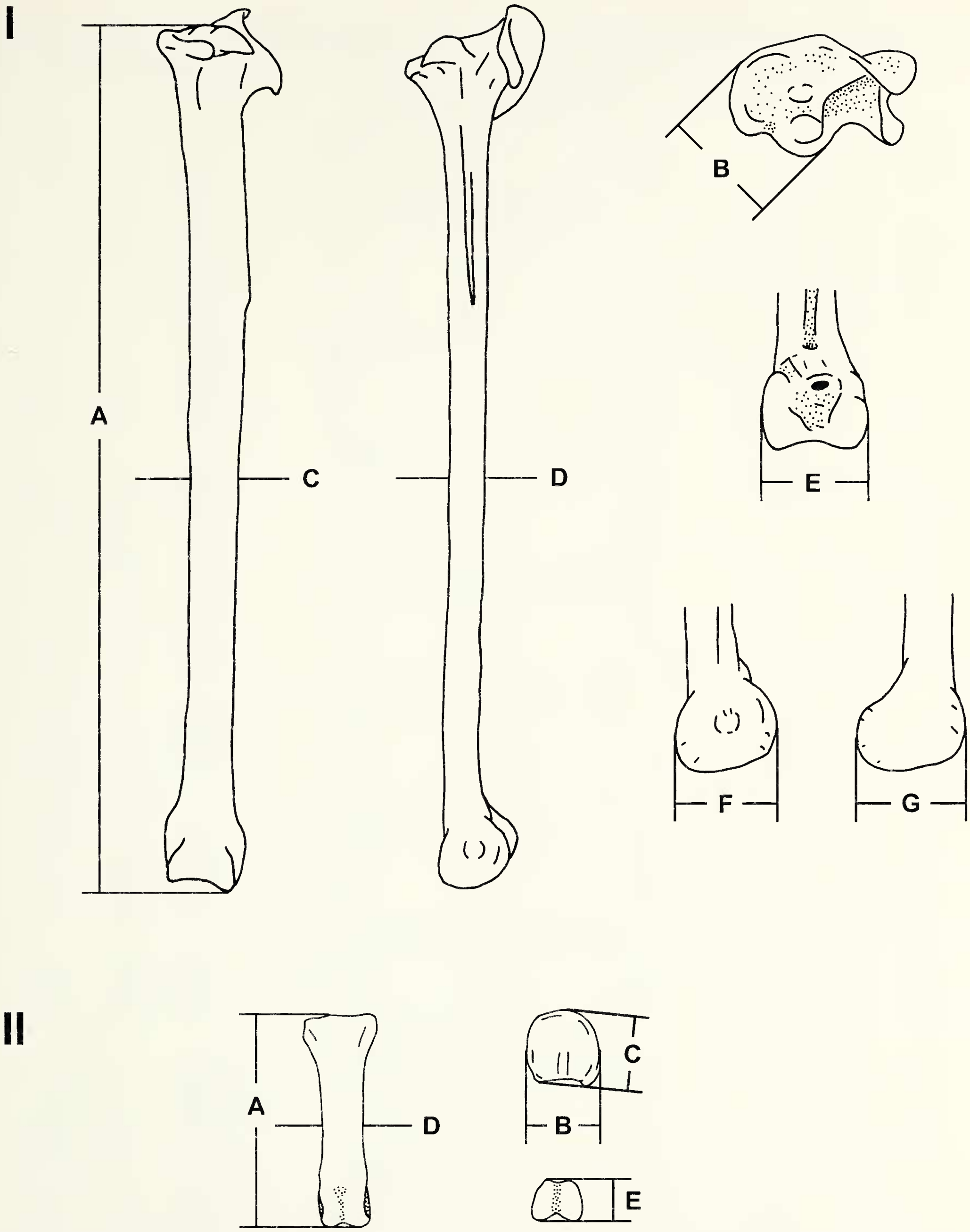


Figure A7 I. Tibiotarsus: measurements (refer to Table A13). A, length without Crista cnemialis, measured between Area interarticularis and Condylus lateralis; B, proximal width, measured between Facies articularis medialis and Facies articularis lateralis; C, maximum (i.e., mediolateral) width at midshaft; D, minimum (i.e., anteroposterior) width at midshaft; E, distal width; F, depth of Condylus lateralis; G, depth of Condylus medialis. II. Pes phalanx 1, digit 3: measurements (refer to Table A15). A, total length, measured between the dorsal edge of the proximal part and both sides of the Trochlea articularis; B, proximal width; C, proximal depth, measured with the plantar side flat against the calipers; D, width at midshaft; E, distal depth

Table A1 Premaxilla: measurements (as in Fig. A1 I)

Measurement	N	Min	Max	Mean	SD
		M. californica (sexes pooled)			
A	22	13.33	16.60	14.99	1.01
B	17	12.10	15.19	13.99	0.89
C	20	4.72	6.55	5.72	0.50
D	20	2.61	4.03	3.58	0.33
		M. ocellata (sexes pooled)			
A	16	14.17	18.96	16.10	1.39
B	15	10.87	14.38	12.54	0.95
C	15	5.94	7.37	6.58	0.40
D	16	2.55	3.69	3.14	0.28
		M. gallopavo (sexes and subspecies pooled)			
A	39	14.50	21.69	18.09	2.10
B	38	11.92	17.07	14.14	1.50
C	39	6.06	8.75	7.21	0.73
D	40	2.45	4.46	3.45	0.49
		M. gallopavo ♀ (subspecies pooled)			
A	18	14.50	18.14	16.20	1.03
B	18	11.92	15.23	12.88	0.78
C	18	6.06	7.40	6.67	0.38
D	18	2.45	3.75	3.08	0.30
		M. gallopavo ♂ (subspecies pooled)			
A	20	17.28	21.69	19.76	1.24
B	19	13.80	17.07	15.26	1.01
C	20	6.70	8.75	7.64	0.62
D	21	3.10	4.46	3.77	0.41
		M. g. intermedia (sexes pooled)			
A	8	15.68	21.13	18.94	2.14
B	7	12.92	16.47	14.41	1.44
C	8	6.24	8.18	7.15	0.79
D	8	3.04	4.34	3.64	0.54
		M. g. merriami (sexes pooled)			
A	9	14.86	20.60	16.76	1.92
B	10	12.13	16.89	13.62	1.77
C	10	6.06	8.26	7.22	0.70
D	10	2.94	3.98	3.32	0.40
		M. g. osceola (sexes pooled)			
A	7	14.50	19.18	17.46	1.72
B	7	12.46	15.28	13.60	1.11
C	7	6.30	7.36	6.80	0.41
D	7	2.72	3.66	3.15	0.32
		M. g. mexicana (sexes pooled)			
A	4	18.71	20.88	20.24	1.03
B	3	15.53	17.07	16.28	0.77
C	3	8.31	8.75	8.60	0.25
D	4	3.65	4.46	4.16	0.36
		M. g. silvestris (sexes pooled)			
A	11	15.06	21.69	18.18	2.06
B	11	11.92	15.67	14.20	1.20
C	11	6.31	8.30	7.11	0.55
D	11	2.45	3.97	3.37	0.43

Table A2 Mandible: measurements (as in Fig. A1 II)

Measurement	N	Min	Max	Mean	SD
M. californica (sexes pooled)					
A	6	7.30	10.07	8.74	0.98
B	11	4.21	5.15	4.62	0.36
C	8	2.05	2.34	2.15	0.11
D	14	5.99	6.94	6.49	0.30
M. ocellata (sexes pooled)					
A	14	9.15	11.90	9.97	0.79
B	16	3.79	5.37	4.44	0.46
C	16	1.84	3.04	2.42	0.34
D	16	5.61	6.97	6.46	0.43
M. gallopavo (sexes and subspecies pooled)					
A	43	9.03	14.03	11.49	1.33
B	43	4.52	7.23	5.60	0.65
C	41	1.77	2.95	2.16	0.28
D	43	6.29	8.86	7.36	0.68
M. gallopavo ♀ (subspecies pooled)					
A	18	9.03	11.79	10.29	0.85
B	18	4.52	5.43	5.05	0.27
C	17	1.77	2.33	1.93	0.14
D	18	6.29	7.10	6.71	0.24
M. gallopavo ♂ (subspecies pooled)					
A	24	10.36	14.03	12.38	0.87
B	24	5.07	7.23	5.99	0.57
C	23	1.98	2.95	2.33	0.25
D	24	6.95	8.86	7.84	0.47
M. g. intermedia (sexes pooled)					
A	9	9.95	13.46	11.87	1.29
B	9	4.73	6.62	5.65	0.57
C	8	1.79	2.45	2.10	0.22
D	9	6.29	8.22	7.29	0.69
M. g. merriami (sexes pooled)					
A	11	9.04	13.18	11.02	1.56
B	11	4.96	6.50	5.58	0.63
C	10	1.81	2.83	2.13	0.35
D	11	6.55	8.10	7.21	0.57
M. g. osceola (sexes pooled)					
A	8	9.73	12.18	11.14	0.84
B	8	4.52	5.79	5.13	0.45
C	8	1.85	2.57	2.10	0.22
D	8	6.31	7.66	7.03	0.59
M. g. mexicana (sexes pooled)					
A	4	11.52	14.03	12.68	1.04
B	4	6.07	7.23	6.76	0.54
C	4	2.27	2.95	2.55	0.30
D	4	7.48	8.86	8.34	0.63
M. g. silvestris (sexes pooled)					
A	11	9.03	13.45	11.47	1.36
B	11	4.82	6.12	5.48	0.43
C	11	1.77	2.42	2.14	0.22
D	11	6.64	8.38	7.44	0.60

Table A3 Skull: measurements (as in Fig. A1 III)

Measurement	N	Min	Max	Mean	SD
M. californica (sexes pooled)					
A	18	41.71	46.00	44.49	1.28
B	29	23.12	26.80	24.92	1.00
C	18	12.99	16.06	15.03	0.77
D	25	32.25	39.19	36.06	1.84
E	9	33.80	39.29	36.60	2.04
F	38	25.80	29.73	28.07	0.95
G	17	26.04	29.73	28.26	1.16
M. ocellata (sexes pooled)					
A	12	40.77	46.84	43.59	1.96
B	12	22.86	26.48	25.32	1.10
C	12	14.69	16.80	15.79	0.71
D	12	32.61	38.24	35.52	1.64
E	12	31.42	37.50	34.52	1.90
F	12	25.21	28.19	26.90	0.97
G	12	25.17	29.42	27.26	1.27
M. gallopavo (sexes and subspecies pooled)					
A	38	43.26	51.70	47.54	2.67
B	39	24.50	29.59	26.93	1.39
C	38	14.16	19.41	16.58	1.51
D	37	33.86	41.66	38.41	2.16
E	36	34.90	46.98	40.82	3.37
F	39	26.62	33.25	29.74	1.73
G	39	26.64	35.11	30.19	2.18
M. gallopavo ♀ (subspecies pooled)					
A	15	43.26	46.55	44.62	0.86
B	16	24.50	26.74	25.56	0.58
C	16	14.16	16.06	15.25	0.69
D	15	33.86	38.14	36.17	1.19
E	14	34.9	40.06	37.25	1.60
F	16	26.62	28.95	28.08	0.80
G	16	26.64	29.60	28.00	0.90
M. gallopavo ♂ (subspecies pooled)					
A	22	46.75	51.70	49.51	1.39
B	22	26.48	29.59	27.97	0.80
C	21	15.39	19.41	17.52	1.19
D	21	38.46	41.66	40.02	0.96
E	21	40.03	46.98	43.23	1.78
F	22	28.60	33.25	30.91	1.17
G	22	29.86	35.11	31.76	1.34
M. g. intermedia (sexes pooled)					
A	8	43.26	51.69	47.76	3.58
B	8	25.04	29.59	27.16	1.60
C	7	15.79	19.37	16.88	1.38
D	8	35.61	41.26	38.14	2.27
E	8	35.42	45.92	40.56	3.77
F	8	26.62	31.79	29.63	2.00
G	8	26.64	33.63	30.05	2.94
M. g. merriami (sexes pooled)					
A	9	43.49	49.74	46.69	2.38
B	10	24.87	29.02	26.50	1.67
C	10	14.16	18.55	15.97	1.49
D	9	34.49	40.65	37.88	2.27
E	8	37.76	44.75	40.99	3.12
F	10	28.20	31.97	29.79	1.61
G	10	27.01	32.90	29.74	2.02

Table A3 Continued

Measurement	N	Min	Max	Mean	SD
		M. g. osceola (sexes pooled)			
A	8	44.01	49.32	46.61	2.21
B	8	25.62	28.77	26.91	1.01
C	8	14.37	18.32	16.15	1.45
D	7	33.86	40.47	37.70	2.50
E	7	34.90	42.70	38.60	3.29
F	8	26.88	30.73	28.89	1.37
G	8	27.68	31.68	29.46	1.37
		M. g. mexicana (sexes pooled)			
A	3	48.03	51.70	50.05	1.86
B	3	25.89	29.24	27.79	1.72
C	3	17.98	19.41	18.85	0.77
D	3	38.17	40.90	39.41	1.38
E	3	40.41	46.98	44.34	3.47
F	3	30.59	33.25	32.32	1.50
G	3	30.86	35.11	33.08	2.13
		M. g. silvestris (sexes pooled)			
A	10	43.84	50.70	48.12	2.39
B	10	24.50	28.10	26.92	1.19
C	10	14.59	18.68	16.64	1.32
D	10	35.85	41.66	39.32	1.86
E	10	36.44	44.22	41.39	2.68
F	10	26.66	31.20	29.69	1.45
G	10	27.04	32.43	30.48	1.81

Table A4 Sternum: measurements (as in Fig. A2 I)

Measurement	N	Min	Max	Mean	SD
		M. californica ♀			
A	17	30.65	35.89	33.23	1.41
B	17	8.95	10.82	9.85	0.59
C	2	70.81	80.15	75.48	6.60
		M. californica ♂			
A	39	39.01	45.46	41.45	1.64
B	38	11.32	13.49	12.46	0.58
C	3	93.25	99.98	97.31	3.58
		M. californica (sexes pooled)			
A	57	30.65	45.46	38.92	4.09
B	68	8.95	13.72	11.69	1.32
C	5	70.81	99.98	88.58	12.66
		M. ocellata (sexes pooled)			
A	15	30.17	37.78	34.18	2.58
B	16	9.61	13.42	11.41	1.15
C	16	68.24	96.83	83.23	9.15
		M. gallopavo (sexes and subspecies pooled)			
A	43	35.72	55.21	45.00	6.27
B	44	9.60	15.00	12.20	1.52
C	42	70.96	124.33	96.63	15.96
		M. gallopavo ♀ (subspecies pooled)			
A	18	35.72	41.32	38.33	1.83
B	19	9.60	12.35	10.76	0.72
C	17	70.96	85.84	79.03	4.13
		M. gallopavo ♂ (subspecies pooled)			
A	24	44.99	55.21	50.07	2.77
B	24	12.05	15.00	13.38	0.84
C	24	100.60	124.33	109.48	6.12
		M. g. intermedia (sexes pooled)			
A	9	35.91	53.40	45.05	7.38
B	9	10.21	14.27	12.16	1.58
C	9	70.96	116.99	94.33	18.82
		M. g. merriami (sexes pooled)			
A	8	35.97	49.55	43.69	5.24
B	8	9.60	13.78	11.47	1.69
C	8	74.82	104.37	89.47	14.07
		M. g. osceola (sexes pooled)			
A	6	35.72	47.54	42.76	5.37
B	6	10.34	12.97	11.94	1.13
C	6	76.74	116.63	98.81	15.33
		M. g. mexicana (sexes pooled)			
A	8	38.97	55.21	47.30	6.74
B	9	10.45	14.31	12.24	1.39
C	7	82.20	114.25	99.23	13.45
		M. g. silvestris (sexes pooled)			
A	11	36.80	53.91	45.94	6.64
B	11	10.47	15.00	12.96	1.59
C	11	80.18	124.33	102.15	17.02

Table A5 Coracoid: measurements (as in Fig. A2 II)

Measurement	N	Min	Max	Mean	SD
M. californica ♀					
A	41	73.07	84.87	80.56	2.58
B	48	68.56	79.44	75.55	2.37
C	44	9.65	12.36	10.96	0.66
D	48	25.50	30.32	28.71	0.95
E	48	7.99	10.14	9.17	0.43
F	29	18.23	21.18	19.85	0.89
G	38	5.65	7.90	6.67	0.48
M. californica ♂					
A	47	92.02	106.08	99.73	3.46
B	61	84.61	98.57	93.01	3.08
C	55	11.81	15.44	13.39	0.80
D	61	30.61	38.15	35.48	1.28
E	61	10.36	12.99	11.64	0.58
F	39	20.92	28.96	24.80	1.81
G	39	7.27	9.52	8.48	0.59
M. californica (sexes pooled)					
A	91	73.07	106.08	90.89	10.09
B	109	68.56	98.57	85.32	9.14
C	171	9.65	15.50	12.39	1.46
D	182	25.50	38.15	32.66	3.47
E	173	7.99	13.20	10.61	1.28
F	76	18.23	28.96	22.57	2.84
G	86	5.65	9.52	7.55	1.05
M. ocellata (sexes pooled)					
A	15	77.22	94.69	86.67	6.23
B	16	72.31	89.50	81.73	5.99
C	17	10.28	13.02	11.88	0.98
D	17	26.11	34.10	30.41	2.60
E	15	8.22	11.72	9.94	1.11
F	15	17.32	23.01	20.23	1.61
G	14	6.32	8.75	7.40	0.74
M. gallopavo (sexes and subspecies pooled)					
A	46	81.56	120.68	101.26	12.97
B	47	76.18	112.65	93.88	12.35
C	50	10.68	17.38	13.60	1.90
D	50	28.97	43.17	35.90	4.43
E	50	8.75	13.40	11.04	1.45
F	47	19.53	31.32	25.20	3.43
G	46	5.65	10.26	7.81	1.23
M. gallopavo ♀ (subspecies pooled)					
A	20	81.56	93.26	87.69	3.97
B	21	76.18	87.21	81.29	3.86
C	23	10.68	13.34	11.76	0.68
D	23	28.97	34.27	31.56	1.42
E	23	8.75	10.38	9.66	0.46
F	21	19.53	26.56	22.06	1.83
G	21	5.65	7.74	6.65	0.59
M. gallopavo ♂ (subspecies pooled)					
A	25	103.93	120.68	112.36	4.44
B	25	96.54	112.65	104.73	4.11
C	26	13.58	17.38	15.25	0.84
D	26	36.47	43.17	39.83	1.74
E	26	10.92	13.40	12.31	0.68
F	25	24.54	31.32	27.80	2.00
G	24	7.85	10.26	8.83	0.60

Table A5 Continued

Measurement	N	Min	Max	Mean	SD
		M. g. intermedia (sexes pooled)			
A	9	84.19	117.99	100.50	15.03
B	9	78.24	109.74	93.28	14.42
C	9	10.94	15.88	13.78	1.96
D	9	29.66	41.29	35.60	4.94
E	9	9.35	13.36	11.28	1.50
F	9	20.18	29.55	24.53	3.16
G	7	6.34	9.63	7.85	1.28
		M. g. merriami (sexes pooled)			
A	10	81.56	111.01	94.93	12.62
B	10	76.18	103.97	88.39	11.96
C	11	10.68	15.83	12.70	1.96
D	11	30.03	40.81	34.18	4.25
E	11	8.75	12.99	10.37	1.50
F	10	19.53	28.80	24.45	3.39
G	10	5.65	8.89	7.16	1.24
		M. g. osceola (sexes pooled)			
A	6	83.85	113.30	100.89	12.71
B	7	77.20	105.73	91.85	12.75
C	8	11.24	14.88	13.13	1.55
D	8	28.97	40.23	35.29	4.29
E	8	8.80	13.06	10.88	1.49
F	6	19.55	26.51	23.83	2.92
G	7	5.81	8.83	7.53	1.24
		M. g. mexicana (sexes pooled)			
A	9	91.79	117.67	104.40	10.90
B	9	84.64	108.81	97.06	10.36
C	10	12.22	17.38	14.35	1.92
D	10	32.05	43.17	36.78	4.54
E	10	9.76	12.86	11.28	1.30
F	10	22.14	31.30	26.86	3.12
G	10	6.61	9.57	8.06	1.07
		M. g. silvestris (sexes pooled)			
A	11	88.45	120.68	106.24	13.00
B	11	83.29	112.65	99.02	11.88
C	11	10.73	16.18	14.12	1.90
D	11	31.30	42.88	37.78	4.24
E	11	9.55	13.40	11.57	1.42
F	11	19.69	31.32	25.89	4.06
G	11	6.56	10.26	8.41	1.23

Table A6 Scapula: measurements (as in Fig. A3 I)

Measurement	N	Min	Max	Mean	SD
M. californica ♀					
A	54	18.16	22.97	21.04	1.05
B	54	10.49	13.98	12.09	0.66
C	50	8.25	11.81	9.97	0.69
D	45	5.33	7.24	6.29	0.39
M. californica ♂					
A	55	24.02	28.77	26.01	1.16
B	54	12.88	16.90	15.08	0.79
C	48	10.48	15.15	12.89	0.97
D	49	6.91	9.09	7.78	0.50
M. californica (sexes pooled)					
A	109	18.16	28.77	23.54	2.73
B	140	10.49	17.15	13.48	1.69
C	137	8.25	15.15	11.38	1.61
D	107	5.33	9.09	7.09	0.87
M. ocellata (sexes pooled)					
A	17	18.89	25.49	21.61	1.91
B	17	11.49	15.07	13.09	1.11
C	17	9.30	11.87	10.58	0.83
D	17	6.04	7.89	6.76	0.54
M. gallopavo (sexes and subspecies pooled)					
A	47	21.93	32.49	27.42	3.28
B	47	12.34	18.87	15.36	1.83
C	47	10.07	15.50	12.91	1.63
D	47	5.92	9.57	7.53	0.94
M. gallopavo ♀ (subspecies pooled)					
A	20	21.93	25.35	23.95	0.93
B	20	12.34	14.21	13.49	0.58
C	20	10.07	12.53	11.28	0.67
D	20	5.92	7.00	6.58	0.34
M. gallopavo ♂ (subspecies pooled)					
A	26	28.15	32.49	30.14	1.32
B	26	15.28	18.87	16.84	0.90
C	26	13.02	15.50	14.23	0.67
D	26	7.28	9.57	8.25	0.54
M. g. intermedia (sexes pooled)					
A	9	21.93	31.95	27.19	4.13
B	9	12.34	18.04	15.06	2.07
C	9	10.07	15.14	12.60	2.13
D	9	6.04	8.08	7.21	0.83
M. g. merriami (sexes pooled)					
A	8	23.23	29.76	26.69	2.84
B	8	13.31	16.86	14.89	1.35
C	8	11.02	14.62	12.76	1.58
D	8	6.45	8.39	7.40	0.77
M. g. osceola (sexes pooled)					
A	8	22.78	29.58	26.52	2.87
B	8	12.62	17.09	14.93	1.94
C	8	10.82	13.99	12.85	1.20
D	8	5.92	8.32	7.34	0.99
M. g. mexicana (sexes pooled)					
A	10	24.13	32.49	27.96	3.41
B	10	13.57	18.06	15.83	1.99
C	10	10.93	14.77	12.54	1.50
D	10	6.74	9.00	7.91	0.98
M. g. silvestris (sexes pooled)					
A	11	23.57	31.57	28.55	3.22
B	11	13.50	18.87	15.96	1.85
C	11	11.20	15.50	13.75	1.61
D	11	6.39	9.57	7.77	1.07

Table A7 Humerus: measurements (as in Fig. A3 II)

Measurement	N	Min	Max	Mean	SD
M. californica ♀					
A	43	106.41	121.44	114.44	3.04
B	36	29.15	33.32	31.50	0.98
C	43	12.54	13.99	13.30	0.39
D	42	11.45	14.01	12.40	0.53
E	43	8.57	11.12	9.48	0.50
F	39	23.03	26.03	24.46	0.61
G	36	11.54	13.11	12.48	0.37
H	38	10.45	13.29	12.23	0.56
I	36	7.71	9.18	8.56	0.34
M. californica ♂					
A	68	128.06	146.95	137.55	4.31
B	65	36.13	41.87	38.62	1.41
C	64	15.23	18.30	16.59	0.69
D	68	13.58	16.47	15.08	0.72
E	68	10.47	13.12	11.81	0.59
F	67	26.87	31.51	29.56	0.93
G	59	14.16	16.74	15.36	0.58
H	63	13.28	16.40	14.87	0.63
I	60	9.14	11.61	10.58	0.54
M. californica (sexes pooled)					
A	111	106.41	146.95	128.60	11.95
B	182	29.15	42.14	35.93	3.73
C	188	12.48	18.30	15.18	1.72
D	201	10.57	16.47	13.76	1.47
E	200	8.03	13.12	10.69	1.26
F	224	22.61	31.51	27.73	2.57
G	211	11.54	16.74	14.30	1.47
H	216	10.45	16.40	13.90	1.37
I	206	7.71	11.82	9.86	1.05
M. ocellata (sexes pooled)					
A	15	107.56	133.39	119.69	8.24
B	15	28.29	38.22	33.19	2.95
C	15	11.70	16.04	13.90	1.27
D	15	11.43	14.73	12.88	0.97
E	15	8.54	11.43	9.91	0.80
F	15	21.89	29.18	25.42	2.04
G	15	12.35	16.28	14.02	1.14
H	15	11.15	15.01	13.09	1.07
I	15	8.15	11.20	9.67	0.87
M. gallopavo (sexes and subspecies pooled)					
A	44	116.22	163.20	138.18	15.57
B	44	32.25	45.78	38.88	4.51
C	45	13.44	20.02	16.73	2.03
D	43	12.27	17.61	14.84	1.52
E	44	9.50	14.00	11.35	1.25
F	45	23.50	34.99	29.31	3.28
G	45	12.62	18.58	15.52	1.87
H	45	12.41	17.46	14.85	1.68
I	45	8.47	12.74	10.47	1.25
M. gallopavo ♀ (subspecies pooled)					
A	20	116.22	129.75	122.41	4.15
B	20	32.25	36.59	34.35	1.23
C	20	13.44	16.20	14.70	0.78
D	20	12.27	14.30	13.41	0.52
E	20	9.50	10.82	10.18	0.41
F	20	23.50	27.70	26.01	1.11
G	20	12.62	14.94	13.63	0.63
H	20	12.41	14.01	13.18	0.52
I	20	8.47	10.02	9.25	0.48

Table A7 Continued

Measurement	N	Min	Max	Mean	SD
M. gallopavo ♂ (subspecies pooled)					
A	23	141.03	163.20	152.10	5.35
B	23	40.51	45.78	42.89	1.69
C	24	17.11	20.02	18.45	0.84
D	22	14.88	17.61	16.17	0.75
E	23	11.13	14.00	12.39	0.70
F	24	30.18	34.99	32.10	1.39
G	24	15.25	18.58	17.12	0.76
H	24	14.36	17.46	16.26	0.83
I	24	10.37	12.74	11.49	0.66
M. g. intermedia (sexes pooled)					
A	9	116.22	155.77	136.63	18.12
B	9	32.42	45.08	38.65	5.23
C	9	13.44	19.01	16.54	2.31
D	9	12.84	16.66	14.91	1.50
E	9	9.72	12.97	11.61	1.19
F	9	24.75	33.08	29.04	3.54
G	9	12.80	17.78	15.26	2.14
H	9	12.78	16.89	14.76	1.72
I	9	8.55	12.66	10.30	1.47
M. g. merriami (sexes pooled)					
A	8	119.26	156.50	135.93	17.33
B	8	32.96	43.64	38.05	4.30
C	8	14.40	18.79	16.32	1.96
D	7	12.46	17.61	14.67	2.12
E	8	9.50	13.27	11.09	1.36
F	8	25.74	33.56	29.33	3.52
G	8	12.62	17.40	15.06	1.92
H	8	12.49	16.74	14.31	1.64
I	8	9.10	11.86	10.35	1.12
M. g. osceola (sexes pooled)					
A	8	118.91	154.34	137.70	14.99
B	7	32.25	42.57	37.89	4.58
C	8	13.44	18.19	16.23	2.06
D	8	12.27	16.18	14.42	1.39
E	8	9.57	12.54	11.14	1.22
F	8	23.50	31.56	28.35	3.39
G	8	13.00	17.01	15.23	1.74
H	8	12.41	16.68	14.56	1.77
I	8	8.47	11.13	10.11	1.19
M. g. mexicana (sexes pooled)					
A	8	125.47	156.50	137.49	12.66
B	8	34.68	44.90	38.75	4.19
C	8	15.48	19.75	17.23	1.74
D	8	13.70	17.00	14.91	1.26
E	8	9.85	12.90	11.07	1.09
F	8	26.99	34.99	29.74	3.38
G	8	13.92	18.58	15.78	1.76
H	8	13.46	17.37	15.07	1.55
I	8	9.46	12.74	10.68	1.29
M. g. silvestris (sexes pooled)					
A	10	122.60	163.20	143.82	16.26
B	11	34.93	45.78	40.84	4.44
C	11	14.62	20.02	17.42	2.11
D	10	13.12	17.44	15.31	1.57
E	10	9.81	14.00	11.82	1.43
F	11	25.52	33.86	30.19	3.13
G	11	13.32	18.54	16.24	1.92
H	11	12.89	17.46	15.53	1.79
I	11	8.77	12.66	10.86	1.33

Table A8 Ulna: measurements (as in Fig. A4 I)

Measurement	N	Min	Max	Mean	SD
M. californica ♀					
A	57	102.97	118.86	109.97	3.16
B	54	16.29	21.28	19.51	1.02
C	57	13.39	16.80	15.62	0.83
D	56	11.76	14.84	13.56	0.65
E	57	6.05	7.18	6.68	0.27
F	57	7.56	9.08	8.30	0.34
G	57	13.22	15.67	14.40	0.48
H	56	11.10	13.07	12.03	0.48
I	56	9.32	11.91	10.50	0.53
M. californica ♂					
A	91	123.92	140.51	132.50	3.85
B	82	20.74	25.67	23.97	1.08
C	90	17.19	20.76	19.09	0.75
D	90	14.51	18.60	16.53	0.67
E	91	7.31	9.27	8.32	0.38
F	91	9.28	11.24	10.20	0.45
G	91	15.67	18.79	17.46	0.63
H	89	13.23	16.28	14.77	0.64
I	89	11.14	13.39	12.32	0.48
M. californica (sexes pooled)					
A	148	102.97	140.51	123.82	11.57
B	171	16.29	26.11	22.39	2.40
C	195	13.39	20.76	17.92	1.78
D	198	11.76	18.60	15.48	1.53
E	223	5.90	9.27	7.61	0.89
F	223	7.38	11.44	9.39	1.01
G	263	12.90	19.00	16.19	1.64
H	258	10.37	16.28	13.62	1.44
I	254	9.32	14.15	11.64	1.10
M. ocellata (sexes pooled)					
A	17	107.89	136.40	120.51	8.79
B	17	20.37	25.44	22.67	1.67
C	17	15.71	19.85	17.58	1.29
D	17	12.01	16.73	14.06	1.25
E	17	6.19	7.90	7.01	0.54
F	17	8.54	10.62	9.68	0.77
G	17	13.36	17.80	15.23	1.26
H	17	11.39	15.37	12.98	1.15
I	17	8.94	12.03	10.27	0.91
M. gallopavo (sexes and subspecies pooled)					
A	43	113.34	159.00	136.39	16.20
B	44	19.59	31.18	24.91	3.40
C	44	15.41	22.75	18.98	2.23
D	44	13.39	19.56	16.53	2.00
E	43	6.77	9.95	8.36	0.95
F	43	8.57	12.55	10.45	1.23
G	44	14.86	21.71	17.87	2.06
H	44	12.34	18.53	15.06	1.81
I	43	9.77	15.01	12.09	1.32
M. gallopavo ♀ (subspecies pooled)					
A	20	113.34	127.47	120.21	4.19
B	20	19.59	23.75	21.56	1.22
C	20	15.41	18.47	16.77	0.80
D	20	13.39	15.88	14.59	0.76
E	20	6.77	8.12	7.45	0.36
F	20	8.57	10.07	9.28	0.42
G	20	14.86	17.13	15.82	0.68
H	20	12.34	14.10	13.29	0.54
I	20	9.77	11.91	10.88	0.55

Table A8 Continued

Measurement	N	Min	Max	Mean	SD
M. gallopavo ♂ (subspecies pooled)					
A	22	141.38	159.00	151.36	4.79
B	23	25.23	31.18	27.82	1.51
C	23	19.28	22.75	20.89	0.93
D	23	16.92	19.56	18.23	0.94
E	22	8.58	9.95	9.19	0.42
F	22	10.29	12.55	11.52	0.58
G	23	18.41	21.71	19.68	0.82
H	23	15.11	18.53	16.61	0.89
I	22	11.90	15.01	13.17	0.77
M. g. intermedia (sexes pooled)					
A	8	113.34	154.31	132.66	19.11
B	8	19.59	27.67	23.67	3.47
C	8	15.41	21.55	18.15	2.48
D	8	13.39	19.40	15.88	2.38
E	8	6.82	9.28	8.23	0.98
F	8	8.74	11.93	10.33	1.26
G	8	14.86	19.93	17.16	2.19
H	8	12.34	16.83	14.50	2.02
I	8	9.77	12.90	11.45	1.30
M. g. merriami (sexes pooled)					
A	8	116.21	157.60	135.75	18.97
B	8	20.39	29.61	24.86	3.90
C	8	16.47	22.30	18.91	2.35
D	8	14.62	19.50	16.85	2.15
E	8	7.16	9.70	8.36	1.07
F	8	8.69	12.55	10.51	1.62
G	8	15.16	20.24	17.75	2.34
H	8	12.86	17.52	14.99	2.10
I	8	10.61	13.72	12.16	1.45
M. g. osceola (sexes pooled)					
A	7	116.82	151.67	135.36	16.26
B	8	20.08	27.21	24.31	2.98
C	8	15.80	20.93	18.77	2.23
D	8	13.44	18.06	15.93	1.88
E	7	7.15	9.46	8.22	0.96
F	7	8.57	11.49	10.05	1.26
G	8	14.90	19.51	17.63	1.94
H	8	13.06	16.64	14.79	1.44
I	7	10.58	13.67	11.91	1.24
M. g. mexicana (sexes pooled)					
A	8	122.91	154.27	135.97	13.74
B	8	21.67	31.18	25.89	3.61
C	8	16.88	22.75	19.42	2.21
D	8	15.22	19.36	16.99	1.78
E	8	7.49	9.95	8.42	0.87
F	8	9.30	11.89	10.48	1.06
G	8	16.59	21.71	18.31	2.02
H	8	13.88	18.53	15.51	1.88
I	8	11.48	15.01	12.62	1.29
M. g. silvestris (sexes pooled)					
A	11	120.78	159.00	141.90	15.32
B	11	21.49	29.73	25.95	3.15
C	11	16.48	22.19	19.70	2.09
D	11	14.64	19.56	17.07	1.93
E	11	6.77	9.90	8.54	1.05
F	11	9.21	12.41	10.81	1.13
G	11	15.68	20.63	18.54	1.99
H	11	13.16	17.85	15.57	1.75
I	11	10.70	14.09	12.38	1.29

Table A9 Radius: measurements (as in Fig. A4 II)

Measurement	N	Min	Max	Mean	SD
M. californica ♀					
A	18	93.90	105.34	98.89	3.62
B	16	8.35	8.98	8.69	0.19
C	16	6.71	7.54	7.10	0.25
D	18	3.69	4.49	4.07	0.22
E	18	9.34	11.05	10.39	0.42
F	18	3.27	4.33	3.62	0.25
M. californica ♂					
A	38	110.19	126.43	118.41	3.41
B	36	9.48	11.59	10.56	0.51
C	37	7.54	9.11	8.47	0.35
D	38	4.19	5.38	4.73	0.31
E	38	11.45	13.12	12.30	0.48
F	38	3.72	4.68	4.34	0.23
M. californica (sexes pooled)					
A	56	93.90	126.43	112.13	9.82
B	152	8.02	12.07	9.84	1.00
C	156	6.14	9.40	7.95	0.78
D	156	3.69	5.50	4.52	0.42
E	263	9.26	13.47	11.56	1.09
F	253	3.15	5.12	4.09	0.42
M. ocellata (sexes pooled)					
A	14	94.45	120.54	106.21	8.33
B	15	7.93	10.65	9.14	0.77
C	15	6.79	8.93	7.67	0.59
D	15	3.52	5.12	4.40	0.42
E	15	9.07	12.52	10.46	0.99
F	15	3.08	4.31	3.72	0.36
M. gallopavo (sexes and subspecies pooled)					
A	43	100.24	142.33	122.63	14.41
B	42	8.57	12.78	10.72	1.35
C	43	7.20	10.55	8.71	0.98
D	43	3.92	5.96	5.01	0.61
E	44	10.40	14.53	12.50	1.38
F	44	3.53	5.14	4.26	0.49
M. gallopavo ♀ (subspecies pooled)					
A	19	100.24	113.80	107.56	3.54
B	19	8.57	10.07	9.37	0.40
C	20	7.20	8.40	7.78	0.32
D	19	3.92	4.75	4.42	0.25
E	20	10.40	11.76	11.11	0.40
F	20	3.53	4.01	3.78	0.15
M. gallopavo ♂ (subspecies pooled)					
A	23	127.74	142.33	135.38	4.26
B	22	10.67	12.78	11.88	0.61
C	22	8.69	10.55	9.56	0.47
D	23	4.86	5.96	5.51	0.29
E	23	12.78	14.53	13.73	0.45
F	23	4.37	5.14	4.69	0.20
M. g. intermedia (sexes pooled)					
A	7	100.24	141.12	121.71	17.97
B	7	8.57	12.71	10.25	1.62
C	7	7.20	9.89	8.38	1.15
D	7	3.92	5.89	5.05	0.70
E	8	10.40	14.12	12.28	1.63
F	8	3.56	5.14	4.22	0.59

Table A9 Continued

Measurement	N	Min	Max	Mean	SD
		M. g. merriami (sexes pooled)			
A	8	103.66	141.61	121.46	17.28
B	8	9.42	12.78	10.98	1.45
C	8	7.65	9.31	8.50	0.75
D	8	4.11	5.94	4.97	0.65
E	8	10.62	14.14	12.35	1.56
F	8	3.53	4.89	4.20	0.56
		M. g. osceola (sexes pooled)			
A	8	104.89	136.30	122.49	13.74
B	8	8.85	11.74	10.42	1.28
C	8	7.42	9.83	8.67	1.06
D	8	4.07	5.67	4.98	0.65
E	8	10.74	13.78	12.52	1.43
F	8	3.76	4.73	4.31	0.43
		M. g. mexicana (sexes pooled)			
A	8	108.83	136.95	121.07	12.20
B	7	9.79	12.52	11.07	1.29
C	8	7.72	10.15	8.76	1.00
D	8	4.28	5.56	4.79	0.44
E	8	11.27	14.53	12.46	1.16
F	8	3.74	4.87	4.14	0.44
		M. g. silvestris (sexes pooled)			
A	11	107.42	142.33	126.64	13.82
B	11	9.19	12.74	10.97	1.29
C	11	7.63	10.55	9.10	1.01
D	11	4.19	5.96	5.22	0.65
E	11	11.39	14.44	12.96	1.25
F	11	3.57	4.95	4.39	0.51

Table A10 Carpometacarpus: measurements (as in Fig. A5 I)

Measurement	N	Min	Max	Mean	SD
M. californica ♀					
A	137	57.61	65.35	61.58	1.77
B	137	54.92	62.68	59.00	1.74
C	122	15.74	19.52	16.94	0.64
D	129	8.51	10.88	9.64	0.43
E	137	4.18	5.70	4.98	0.28
F	92	12.51	15.49	13.92	0.63
G	124	10.41	12.29	11.32	0.41
H	129	8.84	11.38	10.12	0.54
M. californica ♂					
A	212	68.11	77.98	72.85	2.06
B	207	65.03	74.06	69.56	2.00
C	197	17.65	22.11	20.10	0.74
D	202	9.71	12.39	11.06	0.52
E	209	5.29	7.11	6.10	0.34
F	138	14.49	18.20	16.71	0.67
G	178	12.19	14.65	13.36	0.47
H	201	10.61	13.69	12.05	0.63
M. californica (sexes pooled)					
A	351	57.61	77.98	68.42	5.83
B	351	54.92	74.06	65.32	5.50
C	353	15.02	22.11	18.83	1.71
D	368	8.51	12.39	10.48	0.85
E	381	4.18	7.11	5.64	0.64
F	245	12.51	18.20	15.56	1.52
G	320	10.41	14.65	12.53	1.11
H	353	8.84	13.69	11.29	1.11
M. ocellata (sexes pooled)					
A	17	55.99	71.65	63.02	4.84
B	17	53.31	68.43	59.96	4.54
C	17	15.64	21.62	18.53	1.60
D	17	9.06	11.22	10.34	0.72
E	17	4.44	6.05	5.32	0.45
F	17	12.59	17.38	14.82	1.20
G	16	10.50	13.64	12.18	0.95
H	16	9.18	11.81	10.38	0.87
M. gallopavo (sexes and subspecies pooled)					
A	46	61.78	86.15	73.07	8.01
B	46	58.55	81.50	69.39	7.56
C	45	17.46	24.70	20.84	2.19
D	45	9.36	14.19	11.38	1.28
E	46	4.48	6.99	5.75	0.79
F	46	13.38	19.51	16.15	1.92
G	46	11.18	15.72	13.39	1.36
H	46	9.72	15.34	12.66	1.61
M. gallopavo ♀ (subspecies pooled)					
A	23	61.78	69.87	65.60	1.93
B	23	58.55	66.36	62.35	1.87
C	23	17.46	20.50	18.92	0.77
D	22	9.36	11.10	10.24	0.38
E	23	4.48	5.62	5.06	0.31
F	23	13.38	15.59	14.44	0.68
G	23	11.18	13.13	12.16	0.51
H	23	9.72	12.78	11.27	0.77
M. gallopavo ♂ (subspecies pooled)					
A	22	76.49	86.15	80.96	2.67
B	22	72.93	81.50	76.86	2.44
C	21	21.03	24.70	22.91	1.09
D	22	11.46	14.19	12.52	0.74
E	22	5.91	6.99	6.50	0.35
F	22	16.05	19.51	17.94	0.94
G	22	13.96	15.72	14.67	0.53
H	22	12.78	15.34	14.08	0.83

Table A10 Continued

Measurement	N	Min	Max	Mean	SD
		M. g. intermedia (sexes pooled)			
A	7	61.78	82.45	70.57	8.83
B	7	58.61	78.77	66.80	8.36
C	7	17.99	23.55	20.16	2.46
D	7	9.36	12.32	10.79	1.27
E	7	4.70	6.54	5.40	0.74
F	7	13.79	18.21	15.56	1.87
G	7	11.58	14.92	12.89	1.45
H	7	10.81	14.93	12.43	1.86
		M. g. merriami (sexes pooled)			
A	11	61.93	86.15	71.29	9.14
B	11	58.55	81.50	67.73	8.51
C	11	18.20	23.54	20.40	2.13
D	11	10.00	13.68	11.26	1.26
E	11	4.48	6.99	5.47	0.87
F	11	13.52	19.15	15.84	2.21
G	11	11.92	15.09	13.09	1.34
H	11	10.00	14.20	11.71	1.47
		M. g. osceola (sexes pooled)			
A	8	63.52	80.57	73.83	7.04
B	8	60.98	76.69	70.43	6.67
C	7	17.46	22.03	20.00	1.84
D	8	10.00	12.71	11.34	1.04
E	8	4.72	6.84	5.96	0.79
F	8	13.94	18.22	16.32	1.75
G	8	11.18	14.50	13.18	1.43
H	8	9.72	14.44	12.69	1.56
		M. g. mexicana (sexes pooled)			
A	8	65.65	83.42	73.19	7.23
B	8	62.46	77.91	69.27	6.74
C	8	19.33	24.70	21.69	2.10
D	8	10.05	13.33	11.38	1.17
E	8	4.95	6.92	5.75	0.69
F	8	14.80	18.95	16.29	1.59
G	8	12.36	15.67	13.64	1.22
H	8	11.42	15.18	13.02	1.51
		M. g. silvestris (sexes pooled)			
A	11	65.18	85.11	76.34	7.95
B	11	61.77	80.44	72.55	7.56
C	11	18.48	24.56	21.74	2.28
D	10	10.30	14.19	12.13	1.45
E	11	5.02	6.93	6.12	0.78
F	11	13.38	19.51	16.81	2.05
G	11	12.11	15.72	14.08	1.31
H	11	11.67	15.34	13.61	1.33

Table A11 Phalanx proximalis digiti majoris: measurements (as in Fig. A5 II)

Measurement	N	Min	Max	Mean	SD
M. californica ♀					
A	34	21.41	24.46	22.79	0.85
B	33	6.71	8.25	7.21	0.33
C	31	6.60	8.17	7.16	0.36
D	32	9.23	10.85	10.02	0.40
E	33	3.74	4.92	4.15	0.25
M. californica ♂					
A	69	24.87	28.33	26.44	0.84
B	65	7.32	9.22	8.50	0.43
C	68	7.76	9.53	8.70	0.55
D	65	11.03	12.96	12.16	0.43
E	59	4.27	5.71	4.92	0.34
M. californica (sexes pooled)					
A	103	21.41	28.33	25.24	1.92
B	99	6.71	9.22	8.06	0.72
C	101	6.31	9.53	8.19	0.85
D	97	9.23	12.96	11.46	1.09
E	93	3.74	5.71	4.64	0.48
M. ocellata (sexes pooled)					
A	16	21.67	27.25	24.29	1.70
B	14	7.06	9.01	7.79	0.64
C	14	6.77	8.49	7.71	0.64
D	16	9.13	12.06	10.66	0.92
E	14	4.21	5.50	4.89	0.44
M. gallopavo (sexes and subspecies pooled)					
A	46	23.02	31.73	27.27	2.64
B	46	6.97	10.78	8.51	0.89
C	46	7.12	9.82	8.31	0.84
D	46	9.85	14.06	11.66	1.24
E	46	4.07	5.97	4.90	0.47
M. gallopavo ♀ (subspecies pooled)					
A	23	23.02	26.09	24.88	0.80
B	23	6.97	8.25	7.75	0.37
C	23	7.12	8.17	7.56	0.34
D	23	9.85	11.58	10.59	0.46
E	23	4.07	5.12	4.51	0.25
M. gallopavo ♂ (subspecies pooled)					
A	22	27.09	31.73	29.81	1.08
B	22	8.58	10.78	9.31	0.53
C	22	8.66	9.82	9.10	0.35
D	22	11.70	14.06	12.79	0.70
E	22	4.86	5.97	5.32	0.25
M. g. intermedia (sexes pooled)					
A	7	23.02	30.06	26.48	2.71
B	7	6.97	9.39	8.14	1.01
C	7	7.18	8.92	7.98	0.77
D	7	10.32	12.53	11.21	0.91
E	7	4.07	5.28	4.63	0.41
M. g. merriami (sexes pooled)					
A	11	23.97	31.34	26.91	2.91
B	11	7.40	9.57	8.25	0.89
C	11	7.14	9.45	8.01	0.92
D	11	9.85	13.68	11.18	1.41
E	11	4.11	5.45	4.71	0.49
M. g. osceola (sexes pooled)					
A	8	23.47	29.98	27.39	2.40
B	8	7.21	8.94	8.32	0.67
C	8	7.12	8.95	8.29	0.80
D	8	9.94	12.78	11.62	1.12
E	8	4.41	5.38	5.03	0.42

Table A11 Continued

Measurement	N	Min	Max	Mean	SD
M. g. mexicana (sexes pooled)					
A	8	24.24	30.44	27.09	2.48
B	8	8.09	9.90	8.73	0.73
C	8	7.94	9.82	8.59	0.85
D	8	10.74	13.54	11.94	1.21
E	8	4.19	5.66	4.90	0.49
M. g. silvestris (sexes pooled)					
A	11	24.20	31.73	28.43	2.71
B	11	7.72	10.78	9.03	0.97
C	11	7.33	9.63	8.69	0.75
D	11	10.35	14.06	12.31	1.25
E	11	4.48	5.97	5.18	0.44

Table A12 Femur: measurements (as in Fig. A6 I)

Measurement	N	Min	Max	Mean	SD
M. californica ♀					
A	31	98.73	109.15	103.66	2.74
B	39	91.16	99.65	95.95	2.22
C	35	22.93	26.19	25.04	0.83
D	36	8.09	9.87	9.22	0.38
E	39	7.22	9.20	8.19	0.43
F	39	8.97	11.09	10.10	0.46
G	37	20.26	23.25	21.66	0.72
H	30	16.36	19.13	17.55	0.72
I	35	15.95	18.00	17.13	0.59
M. californica ♂					
A	55	113.68	132.03	123.50	3.34
B	67	106.10	122.14	113.12	3.16
C	59	28.01	33.34	30.67	1.25
D	62	10.20	12.85	11.17	0.55
E	66	8.90	10.74	9.90	0.41
F	65	10.62	13.24	12.05	0.49
G	58	24.86	29.09	26.97	0.88
H	54	19.62	23.83	21.70	0.99
I	54	19.18	23.34	21.27	0.81
M. californica (sexes pooled)					
A	97	98.73	132.03	115.99	9.87
B	111	91.16	122.14	106.60	8.64
C	174	22.93	33.34	28.33	3.10
D	174	8.09	12.85	10.38	1.14
E	137	7.22	10.74	9.23	0.94
F	136	8.97	13.32	11.28	1.09
G	173	20.26	29.79	25.11	2.73
H	148	15.69	23.83	20.17	2.21
I	165	15.68	23.57	19.67	2.22
M. ocellata (sexes pooled)					
A	16	96.71	117.09	106.68	6.79
B	16	89.40	107.45	98.04	5.95
C	16	21.19	27.63	24.72	2.11
D	16	7.73	10.39	9.17	0.88
E	16	7.41	9.75	8.82	0.76
F	16	9.08	11.22	10.26	0.68
G	16	18.75	25.94	22.18	2.11
H	16	15.58	20.47	18.18	1.68
I	16	15.98	21.13	18.44	1.61
M. gallopavo (sexes and subspecies pooled)					
A	45	107.03	148.36	126.86	13.55
B	48	97.88	134.99	115.04	11.92
C	48	23.49	37.98	29.73	3.83
D	47	8.69	14.11	11.02	1.37
E	48	8.22	12.14	10.15	1.12
F	48	10.05	14.75	12.17	1.29
G	48	20.68	31.59	25.65	3.27
H	47	16.54	27.60	21.70	2.76
I	47	16.91	26.29	20.96	2.65
M. gallopavo ♀ (subspecies pooled)					
A	20	107.03	120.01	112.81	3.91
B	23	97.88	112.24	103.67	4.19
C	23	23.49	29.05	26.16	1.41
D	22	8.69	11.13	9.79	0.67
E	23	8.22	10.19	9.12	0.46
F	23	10.05	12.29	11.06	0.67
G	23	20.68	25.03	22.62	1.27
H	23	16.54	21.67	19.29	1.30
I	23	16.91	20.21	18.58	0.96

Table A12 Continued

Measurement	N	Min	Max	Mean	SD
		M. gallopavo ♂ (subspecies pooled)			
A	24	129.46	148.36	138.54	4.94
B	24	116.10	134.99	125.83	4.75
C	24	30.84	37.98	33.15	1.76
D	24	10.92	14.11	12.13	0.78
E	24	10.24	12.14	11.13	0.54
F	24	11.92	14.75	13.24	0.75
G	24	26.13	31.59	28.55	1.52
H	23	21.49	27.60	24.10	1.48
I	23	21.11	26.29	23.34	1.36
		M. g. intermedia (sexes pooled)			
A	9	107.65	141.76	125.03	15.45
B	9	97.88	128.34	113.03	14.00
C	9	25.25	34.05	29.87	4.07
D	9	8.95	12.81	10.95	1.58
E	9	8.34	12.09	10.16	1.37
F	9	10.24	13.89	12.15	1.31
G	9	20.96	29.89	25.33	3.67
H	9	18.30	25.24	21.90	3.05
I	9	17.54	23.49	20.77	2.73
		M. g. merriami (sexes pooled)			
A	10	107.03	140.26	121.48	13.68
B	11	98.21	127.29	110.06	11.43
C	11	23.49	33.32	27.83	3.88
D	10	8.69	12.89	10.58	1.51
E	11	8.22	12.14	9.81	1.28
F	11	10.05	13.99	11.59	1.45
G	11	21.17	29.30	24.46	3.12
H	11	16.54	23.93	19.99	2.72
I	11	16.91	23.36	19.60	2.36
		M. g. osceola (sexes pooled)			
A	8	109.97	139.06	125.94	11.93
B	8	100.15	126.08	114.27	10.54
C	8	24.89	31.91	29.13	3.22
D	8	9.10	11.61	10.57	1.07
E	8	8.59	11.07	9.98	1.01
F	8	10.41	13.29	12.02	1.27
G	8	20.68	27.02	24.80	2.83
H	8	19.37	22.96	21.36	1.51
I	8	17.76	23.54	20.70	2.29
		M. g. mexicana (sexes pooled)			
A	6	119.39	146.28	132.13	11.49
B	8	108.41	132.18	118.18	10.13
C	8	27.68	37.98	31.10	3.69
D	8	10.31	14.11	11.69	1.31
E	8	9.07	11.85	10.30	1.04
F	8	11.73	14.61	12.74	1.07
G	8	24.36	31.59	27.07	2.99
H	8	20.23	27.60	22.74	2.75
I	8	20.01	26.29	22.10	2.58
		M. g. silvestris (sexes pooled)			
A	11	112.91	148.36	132.19	13.65
B	11	103.09	134.99	120.85	12.02
C	11	26.11	36.19	31.29	3.72
D	11	9.38	13.34	11.44	1.26
E	11	9.09	11.72	10.55	0.96
F	11	10.76	14.75	12.52	1.28
G	11	22.31	31.06	26.97	3.34
H	10	18.65	26.32	23.11	2.68
I	10	18.31	25.84	22.21	2.75

Table A13 Tibiotarsus: measurements (as in Fig. A7 I)

Measurement	N	Min	Max	Mean	SD
M. californica ♀					
A	10	164.80	173.50	169.43	2.72
B	10	17.92	20.02	18.93	0.60
C	10	8.50	9.53	9.18	0.30
D	10	6.84	8.09	7.57	0.34
E	10	14.77	17.11	16.14	0.65
F	10	13.51	15.41	14.56	0.68
G	10	15.52	16.75	16.14	0.45
M. californica ♂					
A	24	192.00	212.35	204.06	6.59
B	18	21.81	24.88	23.51	0.79
C	24	10.07	11.95	11.25	0.57
D	24	7.99	9.38	8.87	0.37
E	24	18.97	20.98	19.85	0.53
F	23	16.44	19.28	17.78	0.68
G	23	18.16	20.82	19.53	0.72
M. californica (sexes pooled)					
A	34	164.80	212.35	193.87	17.00
B	88	17.24	25.44	21.70	2.42
C	96	8.50	11.95	10.35	1.06
D	95	6.84	9.38	8.30	0.71
E	339	14.41	21.51	17.73	1.76
F	345	12.96	19.28	16.05	1.58
G	326	14.39	21.04	17.56	1.72
M. ocellata (sexes pooled)					
A	16	153.83	200.00	174.16	13.79
B	16	16.75	22.64	19.79	1.74
C	16	8.53	11.12	9.87	0.88
D	16	6.96	8.57	7.91	0.57
E	16	14.44	20.01	16.58	1.54
F	16	13.22	17.28	15.16	1.21
G	16	14.22	19.05	16.46	1.55
M. gallopavo (sexes and subspecies pooled)					
A	48	168.05	240.10	202.17	24.20
B	47	18.50	27.32	22.28	2.75
C	48	9.02	13.53	11.00	1.21
D	48	7.34	11.37	8.76	0.92
E	47	16.74	23.16	19.47	2.13
F	46	14.68	21.34	17.33	1.83
G	48	16.13	23.42	19.17	2.13
M. gallopavo ♀ (subspecies pooled)					
A	23	168.05	193.70	178.26	7.18
B	22	18.50	22.06	19.66	1.06
C	23	9.02	11.02	9.92	0.51
D	23	7.34	8.74	8.00	0.43
E	23	16.74	19.05	17.54	0.75
F	23	14.68	17.03	15.71	0.73
G	23	16.13	19.22	17.22	1.00
M. gallopavo ♂ (subspecies pooled)					
A	24	215.00	240.10	224.77	6.31
B	24	22.86	27.32	24.65	1.25
C	24	10.74	13.53	12.03	0.68
D	24	8.67	11.37	9.50	0.63
E	23	19.34	23.16	21.40	1.07
F	22	17.46	21.34	19.01	0.90
G	24	19.08	23.42	20.97	1.04

Table A13 Continued

Measurement	N	Min	Max	Mean	SD
		M. g. intermedia (sexes pooled)			
A	9	169.85	228.20	200.00	26.58
B	9	18.68	25.03	21.94	2.96
C	9	9.43	12.64	11.08	1.30
D	9	7.48	10.27	8.76	1.05
E	9	16.80	22.33	19.28	2.23
F	9	14.68	19.21	17.05	1.95
G	9	16.20	21.25	18.84	2.28
		M. g. merriami (sexes pooled)			
A	11	168.05	224.10	189.78	24.57
B	11	18.50	25.57	21.12	2.69
C	11	9.02	12.82	10.41	1.29
D	11	7.34	11.37	8.54	1.25
E	11	16.74	23.08	19.04	2.54
F	10	14.90	19.43	16.58	1.67
G	11	16.13	22.28	18.53	2.32
		M. g. osceola (sexes pooled)			
A	8	176.30	227.55	207.78	22.54
B	8	18.58	23.45	21.59	2.19
C	8	9.70	11.97	10.78	0.90
D	8	7.63	9.50	8.65	0.67
E	7	17.03	21.95	19.00	1.94
F	7	14.93	18.70	16.81	1.69
G	8	16.14	20.85	18.48	1.92
		M. g. mexicana (sexes pooled)			
A	8	186.30	240.10	208.01	21.94
B	7	20.64	27.32	23.90	2.55
C	8	10.04	13.53	11.45	1.25
D	8	7.85	10.44	8.96	0.82
E	8	18.47	23.16	20.35	2.00
F	8	16.62	21.34	18.32	1.85
G	8	18.73	23.42	20.53	1.83
		M. g. silvestris (sexes pooled)			
A	11	176.65	235.90	209.86	23.65
B	11	19.31	26.62	23.38	2.77
C	11	9.31	12.82	11.38	1.21
D	11	7.78	10.13	8.92	0.78
E	11	16.76	22.17	19.88	1.93
F	11	15.35	20.30	18.03	1.73
G	11	16.53	22.05	19.71	2.00

Table A14 Tarsometatarsus: measurements (as in Fig. A6 II)

Measurement	N	Min	Max	Mean	SD
M. californica ♀					
A	194	102.61	122.48	115.69	3.51
B	170	16.33	19.81	18.27	0.63
C	181	10.15	12.49	11.37	0.44
D	187	6.23	7.74	6.95	0.33
E	191	4.16	5.35	4.73	0.23
F	179	16.9	20.07	18.68	0.65
G	176	9.04	11.37	10.24	0.47
H	182	8.07	10.05	9.15	0.37
I	—	—	—	—	—
J	—	—	—	—	—
M. californica ♂					
A	196	127.29	150.75	140.82	4.52
B	179	18.60	24.23	21.80	0.99
C	183	11.95	15.29	13.74	0.60
D	194	7.14	9.68	8.54	0.48
E	194	4.89	6.34	5.64	0.28
F	188	20.59	24.63	22.40	0.77
G	183	10.23	13.42	12.33	0.61
H	177	9.69	11.82	10.90	0.42
I	134	58.38	71.85	65.14	2.53
J	115	11.22	24.24	17.43	2.81
M. californica (sexes pooled)					
A	395	102.61	150.75	128.28	13.14
B	509	16.33	24.23	20.09	1.92
C	528	10.15	15.29	12.57	1.26
D	491	6.23	9.68	7.80	0.87
E	512	4.16	6.43	5.20	0.52
F	484	16.90	24.63	20.61	1.99
G	468	9.04	13.47	11.30	1.17
H	471	8.07	11.91	10.04	0.95
I	175	58.38	71.85	64.99	2.57
J	182	11.22	28.94	17.38	3.01
M. ocellata (sexes pooled)					
A	16	108.42	146.70	126.70	11.59
B	16	17.18	22.17	19.59	1.48
C	16	10.43	13.03	11.89	0.85
D	16	6.30	8.19	7.30	0.63
E	14	4.59	5.89	5.32	0.38
F	16	15.56	21.00	18.06	1.60
G	16	9.74	12.44	11.15	0.82
H	16	8.46	10.74	9.31	0.67
I	9	50.07	62.21	56.69	3.83
J	8	15.20	30.13	23.24	4.85
M. gallopavo (sexes and subspecies pooled)					
A	46	118.16	174.20	147.08	19.56
B	46	18.29	26.15	21.97	2.41
C	46	11.34	16.14	13.54	1.46
D	46	6.85	10.22	8.35	0.92
E	45	4.59	6.92	5.65	0.66
F	45	18.20	27.00	21.67	2.47
G	46	9.66	14.45	11.98	1.44
H	45	8.70	13.25	10.56	1.20
I	21	64.37	79.99	72.58	4.47
J	17	10.19	21.49	16.70	3.13

Table A14 Continued

Measurement	N	Min	Max	Mean	SD
M. gallopavo ♀ (subspecies pooled)					
A	23	118.16	137.78	128.64	5.90
B	23	18.29	21.17	19.80	0.81
C	23	11.34	13.36	12.29	0.59
D	23	6.85	8.58	7.59	0.42
E	23	4.59	5.90	5.13	0.35
F	22	18.20	21.93	19.62	1.15
G	23	9.66	12.15	10.72	0.58
H	22	8.70	10.28	9.47	0.49
I	—	—	—	—	—
J	—	—	—	—	—
M. gallopavo ♂ (subspecies pooled)					
A	22	156.20	174.20	166.35	4.63
B	22	22.21	26.15	24.24	1.07
C	22	13.55	16.14	14.87	0.79
D	22	8.11	10.22	9.14	0.57
E	21	5.35	6.92	6.16	0.41
F	22	21.56	27.00	23.65	1.68
G	22	11.94	14.45	13.27	0.75
H	22	10.53	13.25	11.62	0.60
I	21	64.37	79.99	72.58	4.47
J	17	10.19	21.49	16.70	3.13
M. g. intermedia (sexes pooled)					
A	9	122.91	170.50	147.86	21.79
B	9	18.70	24.57	21.92	2.64
C	9	11.48	16.10	13.64	1.73
D	9	7.07	9.54	8.27	0.97
E	9	4.78	6.48	5.63	0.70
F	9	18.20	24.06	21.44	2.48
G	9	10.33	13.92	12.05	1.56
H	9	8.70	12.25	10.45	1.39
I	5	67.37	75.96	72.22	3.77
J	3	18.84	21.20	19.81	1.23
M. g. merriami (sexes pooled)					
A	9	118.16	164.00	131.42	16.71
B	9	18.29	25.88	20.83	2.70
C	9	11.83	15.83	13.08	1.42
D	9	7.26	9.92	7.90	0.98
E	9	4.59	6.27	5.22	0.58
F	8	18.87	26.32	21.11	3.04
G	9	10.26	14.27	11.24	1.50
H	9	9.01	12.59	10.10	1.32
I	2	68.85	79.99	74.42	7.88
J	2	14.38	16.21	15.30	1.29
M. g. osceola (sexes pooled)					
A	8	131.61	170.60	155.39	17.32
B	8	19.23	24.47	21.94	2.22
C	8	11.34	14.33	13.22	1.34
D	8	7.27	9.65	8.41	0.77
E	7	4.78	6.12	5.47	0.44
F	8	18.41	23.30	20.90	2.03
G	8	9.66	13.58	11.71	1.48
H	8	8.72	11.92	10.41	1.16
I	5	64.37	77.33	71.99	5.09
J	3	15.91	21.49	19.49	3.10

Table A14 Continued

Measurement	N	Min	Max	Mean	SD
		M. g. mexicana (sexes pooled)			
A	8	132.93	170.50	148.10	15.89
B	8	20.54	26.15	22.75	2.40
C	8	12.53	16.14	14.12	1.53
D	8	8.03	10.22	8.88	0.82
E	8	5.20	6.83	6.02	0.67
F	8	20.95	27.00	23.56	2.46
G	8	11.27	14.45	12.69	1.26
H	8	9.98	13.25	11.09	1.15
I	2	71.80	74.43	73.12	1.86
J	2	11.87	14.75	13.31	2.04
		M. g. silvestris (sexes pooled)			
A	11	124.20	174.20	153.48	19.92
B	11	19.34	25.67	22.61	2.15
C	11	11.73	15.91	13.80	1.34
D	11	6.85	9.74	8.41	0.97
E	11	4.66	6.92	5.88	0.68
F	11	18.45	24.97	21.68	2.01
G	11	10.52	14.15	12.35	1.25
H	11	8.96	11.95	10.73	1.03
I	7	65.02	77.23	72.59	5.24
J	7	10.19	18.09	15.54	2.59

Table A15 Pes phalanx 1, digit 3: measurements (as in Fig. A7 II)

Measurement	N	Min	Max	Mean	SD
M. californica ♀					
A	111	22.66	26.38	25.17	0.71
B	109	7.67	10.05	8.74	0.46
C	108	7.73	9.99	8.73	0.40
D	110	4.09	5.28	4.58	0.23
E	109	4.78	6.35	5.65	0.30
M. californica ♂					
A	168	27.27	32.36	29.18	1.03
B	159	9.13	11.78	10.61	0.61
C	163	9.08	11.75	10.57	0.50
D	166	4.58	6.31	5.43	0.32
E	164	5.57	7.57	6.75	0.35
M. californica (sexes pooled)					
A	286	22.66	32.36	27.57	2.14
B	280	7.67	11.78	9.84	1.06
C	281	7.73	11.75	9.82	1.01
D	285	4.09	6.31	5.09	0.50
E	281	4.78	7.57	6.31	0.63
M. ocellata (sexes pooled)					
A	13	23.46	30.25	26.51	2.05
B	15	7.84	10.60	9.22	0.81
C	15	7.96	10.54	9.22	0.67
D	13	4.30	5.60	5.05	0.50
E	13	4.69	6.78	5.63	0.54
M. gallopavo (sexes and subspecies pooled)					
A	44	25.33	34.37	29.82	2.83
B	44	8.52	12.74	10.24	1.16
C	44	8.39	12.43	10.21	1.17
D	44	4.61	6.82	5.46	0.62
E	45	5.43	8.09	6.49	0.68
M. gallopavo ♀ (subspecies pooled)					
A	23	25.33	29.75	27.32	1.05
B	23	8.52	10.17	9.28	0.46
C	23	8.39	10.14	9.23	0.51
D	23	4.61	5.79	5.01	0.34
E	23	5.43	6.70	5.93	0.32
M. gallopavo ♂ (subspecies pooled)					
A	20	30.65	34.37	32.63	0.96
B	20	10.35	12.74	11.34	0.63
C	20	10.45	12.43	11.33	0.54
D	20	5.34	6.82	5.97	0.46
E	21	6.49	8.09	7.09	0.40
M. g. intermedia (sexes pooled)					
A	8	25.33	33.56	29.61	3.55
B	8	8.52	11.33	9.97	1.21
C	8	8.39	11.13	9.88	1.31
D	8	4.73	6.19	5.41	0.64
E	8	5.43	7.21	6.29	0.69
M. g. merriami (sexes pooled)					
A	9	25.68	33.78	28.56	2.75
B	9	8.94	12.37	9.91	1.29
C	9	8.66	12.43	9.94	1.27
D	9	4.62	6.37	5.23	0.66
E	9	5.56	7.71	6.23	0.80
M. g. osceola (sexes pooled)					
A	8	26.74	32.37	30.10	2.26
B	8	8.56	11.37	10.13	1.18
C	8	8.64	11.04	10.07	1.09
D	8	4.61	5.66	5.17	0.39
E	8	5.69	7.22	6.47	0.55

Table A15 Continued

Measurement	N	Min	Max	Mean	SD
		M. g. mexicana (sexes pooled)			
A	8	27.75	34.37	30.66	2.55
B	8	9.69	12.74	10.86	1.19
C	8	9.67	12.42	10.75	1.12
D	8	4.94	6.82	5.91	0.64
E	8	6.26	8.09	6.94	0.65
		M. g. silvestris (sexes pooled)			
A	10	26.11	34.04	30.44	3.09
B	10	9.02	11.90	10.44	0.96
C	10	8.92	12.05	10.52	1.05
D	10	4.68	6.45	5.57	0.61
E	11	5.70	7.26	6.61	0.59